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THE BEHAVIOR OF FUNDULUS, WITH ESPECIAL REFERENCE TO OVERLAND ESCAPE FROM TIDE-POOLS AND LOCOMOTION ON LAND.[1]

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It is difficult for one not familiar with life in the sea to realize what a fierce struggle for existence many of the smaller fishes have to wage. Our common minnows, e. g. Fundulus, are beset on every side with danger. They are continuously hunted from below by many predaceous fishes and from above by various sea-birds. For these creatures the price of existence is indeed eternal vigilance. Owing to this price, no doubt, they are among the most wary of fishes. The least disturbance in the water from below or merely an approaching shadow from above sends them scurrying for places of safety.

For purposes of protection they are usually found in shallow water very near the shore-line. As the tide rises they continuously follow the water inland keeping quite near the edge, and as it ebbs they follow it out again. On the newly covered bottom they are frequently seen rooting in the sand, apparently feeding. Thus the movement in harmony with the tide probably serves them in securing food as well as in protection against enemies. But in following the tide aquatic animals are also exposed to danger, for with the incoming tide they are often directed into depressions in the beach which are of such a nature as to hold water for a considerable time after the tide recedes but not until it rises again. To linger at the shore-line in these pools waiting for the water to recede would mean certain death to most aquatic animals. How does it happen that Fundulus, which is so frequently found in such pools, and ordinarily does remain at the water's edge is rarely if ever caught in them.[2] It was this question that inspired the following experimental observations, all of which were made during the summer of 1914 on a sand beach at Beaufort, N. C.

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[1] Published by permission of the Commissioner of Fisheries.

I shall first give in a general way the results of these observations, all of which were repeated a considerable number of times; then I shall present a few experiments in some detail.

If Fundulus gets into a tide-pool while the tide is rising it usually swims about in a deliberate sort of way, stopping here and there to root in the sand and to play with its companions. This behavior continues until the tide turns or at any rate until it is very nearly high. After that the animals may still swim about much as they did before, but they invariably, every few moments, return to the outlet of the pool and swim out and in again. Thus they continue to test the depth of the water in the outlet, and as soon as it gets too shallow they leave the pool and do not return. This accounts for the fact that they are not caught in these pools under ordinary circumstances.

But what interested me primarily was the behavior observed in pools in which the outlet had been closed before the fishes had escaped. Under such conditions it was found that the behavior depends very largely upon whether the water is running in or out of the pool at the time it is closed.

If the water is running in, nothing phenomenal occurs. The animals may swim about rather rapidly for a few moments, but even if they do, they very soon become quiet and proceed to feed and play in their accustomed manner. This experiment was repeated many times and only in one case was the behavior essentially different from that described, and in this case the tide was very nearly high at the time the pool was closed. The response observed under these conditions lead to some important conclusions that will be stated later in connection with a detailed description of the experiment.

If the water is running out when the pool is closed the behavior of the fish is quite different from what it is if the water is running in. After the pool is closed under these conditions, they first swim about rapidly in various directions for a few

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[2] I have again and again, during the ebbing tide, examined numerous tide-pools, but I have never found Fundulus in any of them after the water had stopped flowing out although in some instances they were still 40 to 50 meters long and contained water 20 to 30 cm. deep.

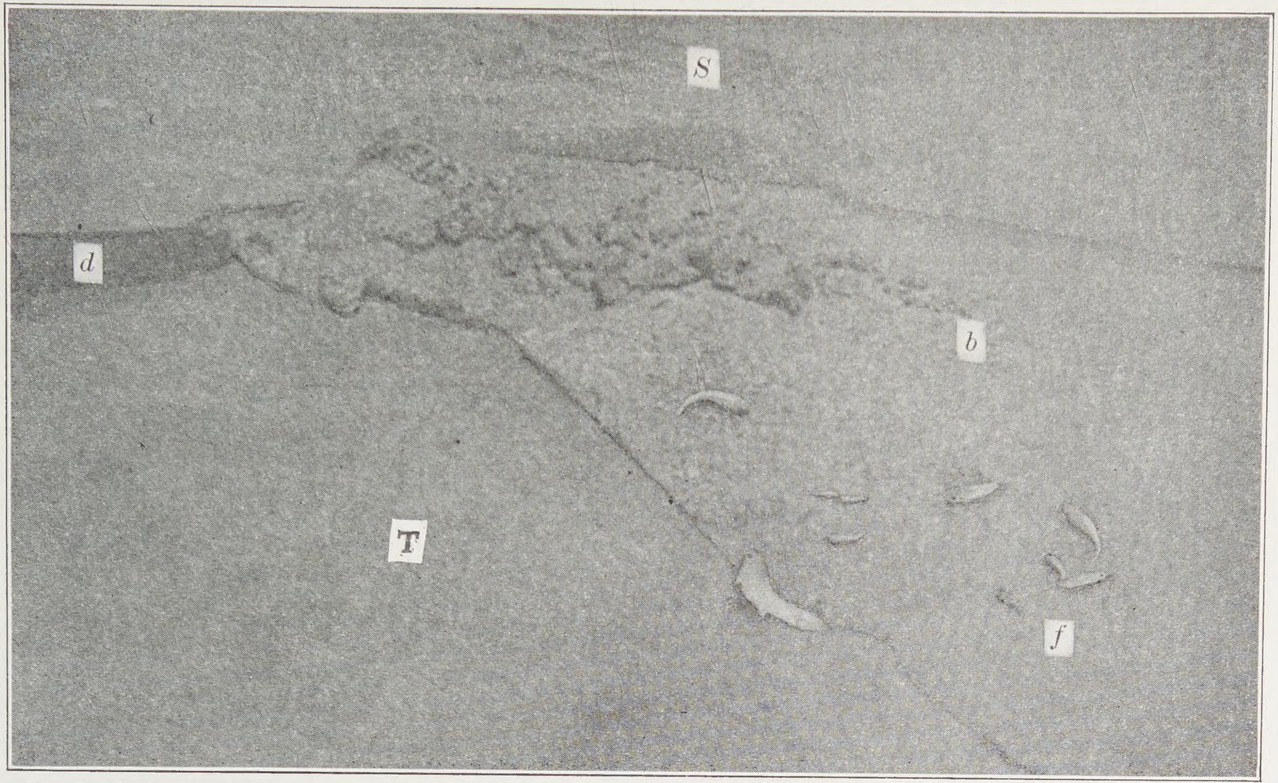

FIG. I. Instantaneous photograph showing a group of ten specimens of Fundulus shortly after they had left a tide-pool. They are traveling over a sand-bar about three meters wide to the sea. f, Fundulus majalis; T, tide-pool; d, dam; b, sand-bar; S, sea. Note that the animals were facing in all directions at the instant the photograph was taken. All were, however, proceeding toward the right.

I am indebted to my friend, W. P. Hay for this photograph.

moments, apparently very much excited; then they usually swim two or three times entirely around the pool keeping very close to the edge much as though they were looking for an outlet; after this a number of them ordinarily crowd together and wriggle well up on the beach into very shallow water. This usually occurs in the original outlet at either end of the dam across it. Finally one flops entirely out of the water onto the sand. Others follow immediately much as sheep follow a leader. After they have left the water they continue flopping and proceed directly across the bar which separates the pool from the sea. (See Fig. I.) Those that are left ordinarily swim about again for a few moments then collect as before, after which more

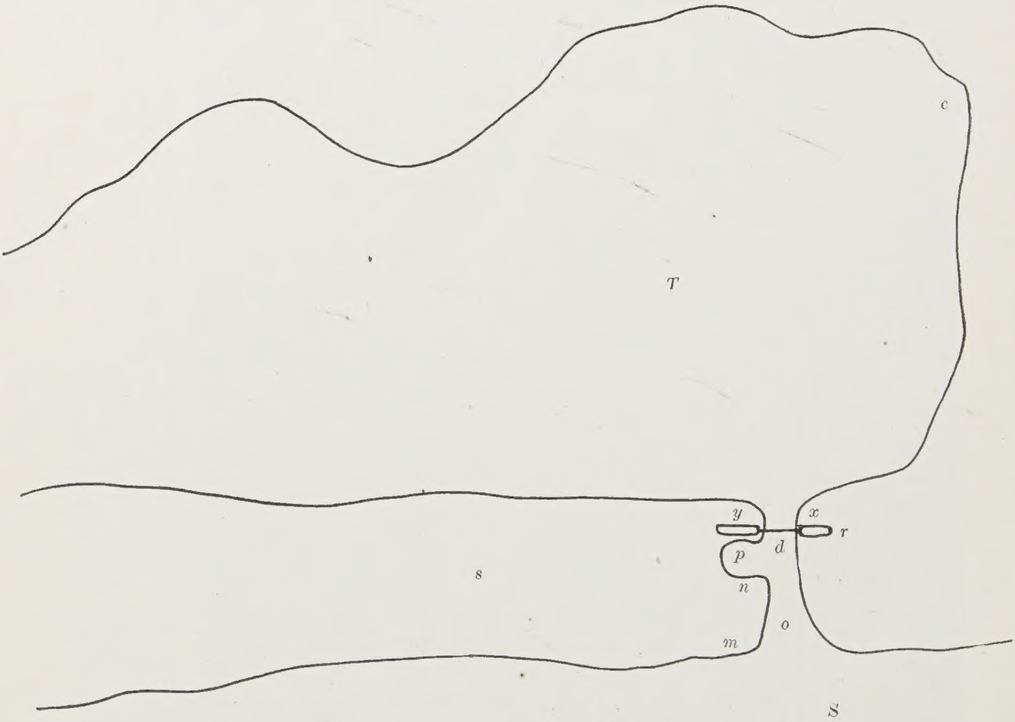

FIG. II. Outline of a portion of a tide-pool with the outlet closed by means of a board. This pool was 50 meters long, 13 meters wide and about 20 cm. deep. It contained approximately 300 specimens of Fundulus, all but 75 of which escaped to the sea by crossing a sand-bar 3 meters wide and fully 10 cm. high. T, tide-pool; o, outlet; S, sea; s, sand-bar; d, dam; r, ridge of sand; p, small pool; c, m, n, x, y, points mentioned in the description.

escape. This is repeated, one group following another, until all or nearly all have escaped.

In this way I have seen more than 200 of these fishes leave a tide-pool 50 meters long, 13 meters wide and 30 cm. deep, and travel across a sand-bar more than 3 meters wide and 10 cm. high, all in the course of half an hour. And I have seen them proceed in a fairly direct course toward the sea even against a moderately strong wind. I have also seen them persistently attempt, continuously for at least a minute, to go overland to the sea against a wind so strong that they could make no headway. When I first saw this performance I was deeply impressed. I had often seen fishes, when thrown on the land, flop back into the water in a more or less aimless fashion, but I had never seen any voluntarily leave a body of water and travel in a coordinate way on land. Concerning the nature of this phenomenon and the regulation in direction of locomotion on land I shall have something to say presently.

The description given above is based upon numerous experimental observations among which the following are typical.

1. On August 30 a tide-pool containing numerous specimens of Fundulus majalis was discovered on a sandy beach. This pool, somewhat irregular in outline, had a maximum length and width of 50 and 13 meters respectively and the water in much of it was, in places, more than 20 cm. deep. A strong current about 3 cm. deep was running out through the outlet, and some of the specimens were continuously passing out or in through it. At 5 P. M. all in the immediate neighborhood were driven in and then the outlet was suddenly closed with a board which extended 5 cm. above the surface of the water. A ridge of sand 60 cm. long and 10 cm. high was thrown up at either end of the board. This ridge extending 16 cm. above the water in the pool, joined on one side of the outlet, a natural bar of sand of the same elevation, so that the pool was separated from the sea on this side by a continuous barrier having an elevation of 15 cm. On the other side however, the natural bar had an elevation of only 5 cm. On this side in the angle between the ridge and the outlet, there was a considerable depression containing a small pool of water connected with the outlet, as represented in figure 2. The sand-bar was at every point over three meters wide. The bank at the edge of the pool

on the sea-side was everywhere very steep, and the water became deep rapidly. On the opposite side the incline was very gradual, and the water was very shallow.

As soon as the pool was closed the fishes began to swim about rapidly in an aimless sort of way. They continued for a few moments, then they came very close to the edge of the water and swam several times up and down the side of the pool nearest to the sea. Finally a dense aggregation formed in the outlet near the dam and soon, three minutes after the outlet was closed, they began to come out in the angle between the outlet and the dam represented by y in figure 2. The first group that left the water consisted of about twelve individuals. All of these followed the ridge from y to its end, and then turned and went toward the sea. Other groups soon followed behaving in a similar way. Many attempted repeatedly to cross the ridge at y and three actually succeeded although the ridge was fully 10 cm. high and the incline over it formed an angle with the horizontal of more than 45 degrees. After passing the ridge some went directly across the sand-bar and entered the sea at m, but many of them got into the small pool p. All of these swam directly across this pool to the bank at n. Here three were seen to leave the water again, climb the relatively steep bank 9 cm. high and then proceed to the sea, although this pool had a free passage to the outlet through which nearly all escaped. This seems to indicate that after these creatures once start in a given direction toward the sea they have a strong tendency to continue in this direction.

About 25 individuals were seen to leave the tide-pool at c, but all returned. A few of these reached a point nearly a meter from the edge of the water before they returned but most of them went only a few centimeters. Quite a number also left the pool at x but all of these returned after going a very short distance.

When the pool was closed there were approximately 300 specimens in it. The following morning 75 dead ones were found; consequently some 225 must have escaped.

2. In all of the experiments made during the falling tide behavior similar to that described above was observed. In some of them, there were, however, additional points of interest. A detailed description of one of these follows.

In this experiment a dam was thrown across a long narrow tide-pool running parallel with the coast-line as shown in figure 3. In this way approximately 150 specimens of Fundulus majalis of various sizes were enclosed. The sand-bar between the pool and the sea varied in height from 10 to 15 cm. This bar rose rapidly along the edge of the pool on the sea side, but on the opposite edge of the pool the inclines was very gradual: so that the elevation at the end of the dam on this side was only 3 cm., while on the sea side it was over 10 cm.

Observations were continued for 20 minutes. During this time nearly 50 specimens escaped by traveling overland around the end of the dam from x to y, i. e. on the land side where the elevation was least. These specimens were opposed in their locomotion on land by a fairly strong wind. A few escaped at the opposite end of the dam, going overland from m to n. And two crossed the sand-bar taking a direct course to the sea. A few also came out a short distance elsewhere but all of these returned to the pool.

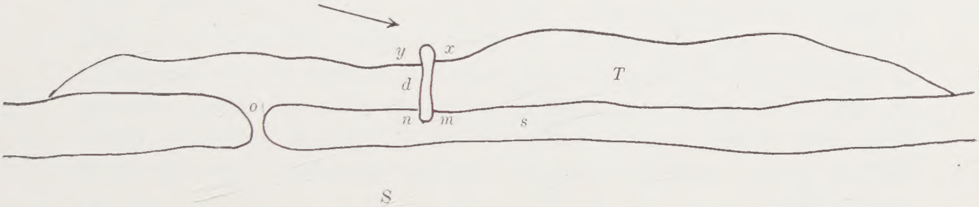

FIG. III. Outline of a long, narrow tide-pool with a dam thrown across near the middle. This pool had a maximum width and length of 2 and 24 meters respectively. It contained approximately 150 funduli, most of which escaped by traveling overland, against a moderately strong wind, around the end of the dam on the land side, xy. T,tide-pool; o, outlet; S, sea; s, sand-bar; d, dam; m, n, x, y, points mentioned in the description. The arrow indicates the direction of the wind.

The results obtained in these two experiments and others show that Fundulus tends to leave the tide-pools near the original outlet. Relatively few were seen to attempt to escape elsewhere in spite of the fact that the incline of the bottom was usually much more gradual in many other places. They also show that there is a tendency to select the lowest place near the outlet. This is particularly evident in experiment 2. Ordinarily these creatures leave the pools on the side of the outlet nearest the sea but in this case they left on the side nearest the land where the elevation was much less than on the opposite side.

The results show, moreover that after the fishes are out on the land they tend to go directly toward the sea. This is evident from the persistent attempts made in experiment 1, to cross the ridge at y, and from the direct course taken after passing the ridge, especially in the small pool p. They show, furthermore, that the tendency to go toward the sea is not a response to the light reflected from the water, for in experiment 1, the fishes, when they were behind the ridge, persistently attempted to go toward the sea, although in this position, the ridge effectively hid the sea from view while the pool was fully exposed. In experiment 2 they also proceeded toward the sea under similar conditions, or rather toward the original outlet of the pool.

3. As previously stated, if the tide flows in when the pool is closed, nothing out of the ordinary occurs in the reactions of Fundulus. Only in one experiment, that described below, was there an exception to this. Unfortunately, owing to other duties, I was unable to repeat this experiment under the same conditions.

On September 7, at 10.19 A. M. the outlet of a large tide-pool (12 by 30 m.) containing about 350 funduli was closed. At this time there was a strong current of water running into the pool indicating that the tide was still rising. Immediately after, the pool was closed, the fishes began to swim about rapidly being apparently very much excited, and two minutes later they began to come out of the water. In short, they behaved precisely as they ordinarily do when the tide is running out, not at all as they ordinarily do when it is running in. They continued to come out for some time, most of them, as usual near the original outlet, but nearly all of them returned to the pool; only a few succeeded in crossing the sand-bar which separated the pool from the sea. The sun was very hot at this time and the sand on the bar rather dry. This probably accounts for the fact that nearly all returned to the pool after proceeding a short distance toward the sea. At 10.40 the tide had unquestionably turned for the water outside the pool was already several centimeters lower than that inside. The tide was consequently very nearly high when the pool was first closed and this no doubt, was the cause of the unusual behavior. If this is true it must be assumed that in some way these animals know when the tide is about to turn, for their method of response changes from that characteristic of the rising tide to that characteristic of the falling tide before the tide turns.

At 11.10, i. e. nearly an hour after the pool was closed, the fishes were much more quiet than they had been earlier, Most of them were swimming about in a leisurely fashion, some were feeding and none were coming out of the water. They were observed for some time after this, but at no time was there the slightest indication of an attempt to leave the water, although various methods were used in trying to make them leave, e. g., boards were thrown into the pool, the water was violently disturbed by running around in it and much of it was drawn off. Later the water in this pool together with the fishes was drained into a lower pool. In this pool the fishes swam about rapidly as though they were considerably excited but none of them left the pool, although a few at different times came out of the water a short distance. Their behavior in general was markedly different from that observed in animals suddenly shut in pools during the ebbing tide . This indicates strongly that the all-important factor involved in the behavior resulting in the overland escape of Fundulus from tide-pools is the sudden closing of the outlet through which it is accustomed to go. The location of this outlet they evidently remember for some time. The results of this experiment show also that Fundulus becomes very rapidly acclimated.

The movement of these fishes on land seems to be well coordinated. They travel in fairly direct courses. There is nothing in the nature of aimless tumbling about as is ordinarily seen in the behavior of fishes out of water. Locomotion consists of successive leaps due to sudden bending of the body. When the fish falls after a leap it may be directed toward any point of the compass, but the succeeding leap carries it on its course no matter in which direction it may be facing at the time of the response. Thus before each leap it may be headed in the direction in which it is traveling or in the opposite direction or in any other direction. It is really remarkable that the bending of the body is so regulated that the animal continues to move in a given direction regardless of its axial position at the beginning of the successive reactions. As to the mechanics of the process I am as yet quite in the dark. And I am also unable to say what factors in the environment serve to direct these animals overland to the sea. Vision of the sea seems to play little or no part in this, for the fishes continue toward the sea if a screen is so placed that the water can not be seen; or if conditions are so arranged that the largest surface of water visible is in the tide-pool. The slope of the beach can also not serve to guide them, for in crossing the sand-bar they have to go up grade as well as down. Nor are there any other external features that seem capable of serving as a guide. The phenomenon is consequently probably very largely dependent upon internal factors.

SUMMARY

1. Fundulus is frequently found in temporary tide-pools, but rarely if ever after the water is so low that the outlet is closed. When the tide is falling it swims out and in at short intervals but as soon as the water in the outlet gets low it does not return. In this way it avoids being caught in these pools and killed when they dry during low tide.

2. If the outlet is closed while the tide is rising nothing out of the ordinary occurs, but if it is closed while the tide is falling the fishes swim about rapidly in various directions for a few moments. Then they come out of the water and travel overland to the sea. Many specimens have been seen thus to leave large tide-pools and travel across sand-bars more than 3 m. wide and 10 cm. high.

3. Fundulus nearly always leaves the pools on the sea side near the original outlet. It apparently remembers the location of the outlet; and it is the sudden closing of this that constitutes the principal factor causing these fishes to leave the pools.

4. On land they never travel in the wrong direction any considerable distance. It is not known how they are guided in the right direction, but it is known that light reflected from the water is not a significant factor in the process.

5. Locomotion on land is brought about by successive leaps due to rapid bending of the body. The course taken is fairly direct. Every leap carries the animal in the right direction, although the axial position at the beginning of the successive leaps varies greatly; the fish, at this time, may be headed in the direction of locomotion or in the opposite direction or in any other direction. The movements appear to be well coordinated, but the process involved in thus regulating the direction of locomotion is not understood.

EXPERIMENTS ON SEX RECOGNITION AND THE PROBLEM OF SEXUAL SELECTION IN DROSOPHILA

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Much has been written on the subject of sexual selection since Darwin first developed the theory, and many remarkable observations have been recorded. There has, however, been very little experimental work in this field. Darwin and those who have followed him have obtained much of their evidence from the insects, and within this group some of the most striking cases of elaborate mating habits have been reported in the Diptera, and here too there is to be found a most remarkable array of secondary sexual characters. Perhaps the most extreme case is that of the *Elaphomyia* described by Wallace, in which the male has long, hornlike processes arising from his head, which are absent in the female. The families of Platypezidae, Dolichopodidae, and Empididae are especially rich in secondary sexual characters, which occur in the legs, wings, antennae, face, or other parts. In the two latter families some very curious observations on mating habits have been recorded (see especially Poulton's account ('13) of Hamm's work on Empididae).[1]

Some of the best experimental evidence in favor of sexual selection is that obtained by Lutz (1911), who worked with an abnormal wing venation in *Drosophila ampelophila* which he found to be strongly selected against. To Dr. Lutz is due the suggestion that the mutants in this fly obtained by Morgan would form excellent material for the study of the problem. The method of some of the experiments was also suggested by Lutz. I took up the matter at the suggestion of Professor Morgan, to whom I am greatly indebted for most of the material and for his encouragement and criticisms. Several discussions of the matter with Dr. Lutz have also been very helpful. Some of the work was done at the Cold Spring Harbor Laboratory in the summer of 1911, and I wish to express my appreciation of the interest in the experiment shown by Dr. C. B. Davenport at that time.

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[1] I have myself observed courtship in a few Dolichopodidae and in a number of other Diptera. These observations will be published in full later.

COURTSHIP AND MATING

Most of my observations on courtship in *Drosophila* have been made upon *D. ampelophila* Loew. In general the process is very similar in *D. busckii* Coq., but differs in several respects in *D. amoena* Loew, *D. repleta* Woll., and *D. funebris* Fabr. The first and most noticeable act in courtship occurs when the male, being near the female, extends one wing at about right angles to his body, and vibrates it for a few seconds. The wing is then returned to the normal position and the process is repeated, usually with the other wing. But between times there is a scissors-like movement of the wings repeated several times. This vibrating of the wings is often repeated many times, and may be done in any position relative to the female, though the male always faces her. Usually, in fact, he swings quickly around her in a semicircle once or oftener during the process. Soon the male begins to protrude his genitalia and, if the female remains quiet, to lick her posterior end. Some white matter now protrudes from her ovipositor, and other males in the same vial are usually observed to become excited now and begin courting; indicating odor as a cause of sexual excitement. If the female runs or flies away the male is excited, moves his wings jerkily, and walks around rapidly, but seems unable to follow the female accurately or to locate her quickly. The penis is directed forward by bending up the abdomen underneath, towards the thorax, and is jerked toward the female (the male always standing facing her at this stage), but not always toward her genitalia, as I have seen it strike her in the eye.[2] If it does strike the mark the male mounts on the female's back, between her wings. Mounting never takes place until after the actual copulation has occurred, in which respect *Drosophila* differs from some related flies (e.g., Muscidae, Anthomyidae, Sepsidae, Borboridae, and Ephydridae, so far as my observations go). In these forms the male flies and lights on the female, after which copulation may or may not take place, probably depending upon the way the female responds.

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[2] The male in this case, however, had white eyes, and so was perhaps blind, Normally the aim is accurate.

Berlese ('02) and Hewett ('08) find that in the house fly the final step in copulation is taken by the female, which inserts the ovipositor into the genital opening of the male. I have not been able to verify this for *Drosophila*, but it is probably true here also. In *Drosophila*, as in some other related flies (I have examined a few Anthomyids and *Sepsis violacea*), the ovipositor enters the male opening, instead of the penis entering the female duct. But I cannot state positively that the female inserts it instead of the male drawing it in by means of his genital armature. In any case, it is certain that the female is not entirely a passive agent. The time required for copulation to take place depends largely upon whether she stands quietly and allows the male to pair, or moves away when he begins to court. In the latter case very active males have been seen to pair while the female was walking away, but this is exceptional. Occasionally a female seems to frighten off a male by spreading her wings and moving quickly toward him.[3] When this happens he moves off, and does not so far as I have seen, then pair with that female, although she has been known to pair with another male within a few minutes afterward. That this is really a threat on the part of the female seems likely from observations of fighting between males. If two males are courting the same female they often grow very excited, especially if she is unwilling to stay quiet. In such cases they may sometimes be seen to spread their wings, run at each other, and apparently butt heads. One of them soon gives up and runs away. If the other then runs at him again within the next few minutes he usually makes off without showing fight.

The time occupied by the process of courtship varies greatly with the age and condition of the flies and with the temperature. Copulation may occur within a few seconds after the flies are put together, with little preliminary courtship. While experimenting with flies about 3 or 4 days old, which had never been allowed to pair, I have found that 20 minutes or a little less is about the average length of time before copulation occurs. The flies may remain *in copula* for only a few seconds, but so far as my observation goes this occurs only after a prolonged courtship in which the female has seemed unwilling to mate, and is, I think, due to the male not getting a good hold. I do not know whether or not such pairings are successful. Ordinarily copulation lasts about 20 minutes.[4]

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[3] Compare Howard's ('02, pp. 141 and 145) accounts of Asilid and Empidid flies eating males which were courting them.

EXPERIMENTS ON OTHER INSECTS

There is a considerable body of evidence relating to the question of sex recognition in the Arthropods. A short review of the subject and a bibliography are given by Chidester ('11), so I shall confine myself here to the evidence dealing with insects. There is evidence from several groups of insects, but most of it points the same way. Sex recognition at a distance is by smell, but the actual process of copulation depends upon the sense of touch.

In the Orthoptera, Stockard ('08) has observed the male walking stick to pair with the detached abdomen of a female which was fastened to a stick with wires for legs.

In Coleoptera, Féré ('98) finds that male cockchafers do not pair if the antennae are removed. Males will sometimes pair with males, provided the latter have just paired with females, or have been artificially impregnated with female juices.

Mast ('12) shows that in the firefly the males find the females by means of the flashing lights, signals being made by both sexes. Tower ('06) reports that in *Leptinotarsa* males normally never try to actually copulate with males, but that if the antennae are removed or painted with shellac they will try to pair with any individual they happen to touch. If this individual is a female pairing will occur. If the abdomens of females are removed the males are attracted by them, though not by the wings, head and thorax. Females with their abdomens coated with shellac are not attractive to the males.

Féré ('98a) found that in the silkworm moth males will pair with other males, which have not been given a chance to get the female odor, if the latter males are sluggish, as after removal of the antennae. Males without antennae will copulate. Kellogg ('07) has since reported that males without antennae find the females only by chance, while normal males go straight to them. If one antenna be removed the male travels in a circular path instead of going toward the female. If a male without antennae happens to touch a female he immediately shows strong sexual excitement, such as normal males show when brought near females. Scent glands on the abdomen of the female were shown to be the seat of the olfactory attraction, for when the abdomens were removed males were attracted by them and not by the rest of the female. Blackening the eyes produced no change in the behavior.

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[4] In 20 cases the duration of copulation was timed with the following result (minutes): ½, 5, 16, 17, 18, 18, 19, 20, 21, 21, 21, 21, 22, 22, 23, 24, 25, 26, 27, 33.

Mayer (1900) performed numerous experiments on the moth *Callosamia Promethea.* He showed that it is odor that attracts the males, and that this odor comes from the abdomen of the female. Interchanging of wings indicated that the marked sexual dimorphism in color, which occurs in this species, has no selective value.

Kirkland (1896)[5] showed that in the Gypsy moth odor is again the main element concerned, but the wings of the female, as well as her abdomen, have an exciting odor. Mayer and Soule (1906) tried experiments on this form, which they supposed indicated that normal females discriminated against males without wings. I find, by applying Yule's (1911) formula for the standard error of the difference, that the difference between the per cent of times winged males paired without resistance and the per cent that wingless males paired without resistance (the measure of sexual selection used by these authors) is almost exactly three times the standard error. This means that the result is not conclusive. Mayer and Soule blinded females and found this apparent discrimation against wingless males to disappear, but the per cent of resistance dropped, as a whole, from 46% in the normal females to 27% in the blinded ones. This may mean that the blinded ones were too greatly disturbed by the blinding to pay much attention to what male mated with them. While I am inclined to suspect that there is some odor connected with the male's wings, still, as stated above, it is not certain that any effect at all is produced by removing the wings of the male. Further evidence against the importance of sight is furnished by the fact that females did not discriminate against males with wings painted in unusual colors.

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[5] I have not seen this paper, but make the statement on the authority of Mayer and Soule (1906).

Federley (1911) gives evidence indicating that odor is a strong sexual stimulator in the moth *Pygaera*, and may even cause males to attempt to pair with the bars of the cage in which they are confined. Entomological literature contains many accounts of the remarkable ability of male moths to locate females though smell. A few of the more striking cases are given by Washburn ('09, pp. 87 and 88.)

SEX RECOGNITION IN DROSOPHILA

It was noted above that when an egg protrudes from the ovipositor of a female any males in the same bottle usually become excited and begin courting. When a female is killed eggs are likely to protrude, and males are often seen vigorously courting females which have been freshly killed, even though the killing agent were so strong smelling a substance as ether. In such cases it is the posterior end of the abdomen which seems to be the chief focus of attraction. The attraction may last for at least 30 minutes after death, and probably longer. I have not as yet been able to cause males to copulate with dead females, probably because the female normally takes an active part, as indicated above.

If a male which has just paired is placed with a male which has been isolated from females for several days he may be courted by that male, though this is not frequent. If two males are kept in solitary confinement for four or five days and are then put together they often court each other, in one case even the doubling up of the abdomen being seen, and the wing movement (*not* fighting) being almost invariably observed. Such mutual courtship between males has not been seen under other conditions, but a dead male which had not been with females for two days before killing has been seen to be courted by other males. This courting, however, seems more likely to occur when juices from female abdomens are put on the dead males. In *Psychoda* sp. courtship of males by males seems to be very frequent, and often copulation is attempted. The genitália even become attached, and stay so for several seconds. Males have been seen to mount males in *Fucellia marina*, *Sepsis violacea*, and *Sarcophaga* sp.

In order to test what part is played by the female juices mentioned above I placed some on bits of filter paper and put these in the same vial with males. The males paid no attention to the paper, and showed no signs of excitement, though that they were sexually ripe was shown by the fact that they courted and paired with females when they were put in with them. This experiment has been repeated several times with the same result. When a female is thoroughly crushed and the remains heaped up in a little pile the males will sometimes court slightly, but as a general rule, the more mashed the female is, the less excited the males become. No great importance is to be placed upon this latter experiment, as the result is complicated by the presence of so many other body juices. This objection, however, will hardly hold in the case of the filter paper impregnated with female juices. The objection that not enough odor was present may perhaps be justifiable in that case. But neither of these objections would seem to apply to the following experiment. Two females were placed in a small, dark, cloth bag and this was put in a vial with a few males. The males were close to the females, which they could not see or touch, but should be able to smell. This experiment was done three times and in no case did the males show any signs of sexual excitement, though in all three cases they did court immediately afterwards when given females in the usual way.

It has been shown by Barrows ('07) that the sense organs for smell in *Drosophila*, insofar as one may judge from reactions to food substances, are located in the terminal antennal joints. For this reason I was led to perform the following experiments, in an effort to determine the part played by the sense of smell in courtship and copulation.

The antennae were removed from several males,[6] which were after several days placed with virgin females. Such males are very sluggish, and it was therefore not surprising that no courtship was observed. However, one such male was found copulating, and at least three of them left offspring after the operation. One of the three had white eyes, and was therefore probably also blind. Courtship has been observed in two males from which the antennal aristae had been removed. A normal male has been seen copulating with a female from which the antennae had been removed, and this pairing resulted in the production of offspring.

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[6] I have found that antennae may easily be removed without using the complex method described by Barrows, if the operation be performed on very young flies.

The above experiments failed to give any evidence demonstrating that smell alone can cause males to show signs of courtship. Another series of experiments, now to be described, has indicated, however, that smell may be a secondary factor in causing sexual excitement. Males and virgin females were isolated for three or four days and were then placed, in pairs, in clean vials. The length of time before copulation occurred was recorded; and, after it had taken place, the flies were removed and a new pair was placed in the same vial. The only difference between the two sets was that one lot was in clean vials, the other was in vials in which copulation had just occurred. In these experiments an equal number of each sort was done on each day (placing a third pair in some vials when necessary in order to get an equal number), and all flies used on a given day were as nearly the same age and size as practicable, and were from the same culture. Table I gives the result of the experiments. It shows that in the first five or six minutes the flies in the used vials are more likely to copulate than are those in the clean vials; between ten and twenty minutes there are more copulations in the clean vials, and after that the two series are parallel. Apparently there are a certain number of pairs that are nearly ready to mate, and these will mate more quickly if another copulation has just occurred in the same vial. But if much courtship is to be required before copu-

TABLE I

Minutes before Copulation	Number of times observed	
	1st pair	2nd pair
1– 3	13	22
4– 6	12	22
7– 9	5	7
10–12	7	6
13–15	11	2
16–18	7	5
19–21	8	5
22–24	4	3
25–27	5	3
28-30	2	1
31–33	7	1
34–36	2	2
37–39	0	2
40 and more, including failures.	24	25

tation, then the effect of smell is negligible. It is not clear from these results whether the effect is produced upon the males, the females, or both.

In order to test whether sight is the sense which stimulates the male I carried out the following experiment. Two vials having the same bore were filled with cotton up to about three centimeters from the mouths, and then placed with their mouths together. A thin glass cover-slip was then placed between them, and a male fly was placed in one vial, a female in the other. These flies had been isolated for several days, and were sexually ripe. The male could see the female, but could not touch or smell her. Once or twice they met " head on " with only the cover-slip between them, but the male showed no signs of recognition. After thirty minutes the female was let in the vial containing the male; and the vials were left in position. He courted her within two minutes, and paired in five minutes. The experiment was repeated with the same result, except that copulation now occurred in three minutes after putting the flies together.

It is also evident that sight is not necessary for pairing from the facts that Drosophila breeds freely in the dark (see Payne, '11), and that pure stock of white-eyed flies (which may be blind) has been kept for many generations.

In *Fucellia marina* and in *Musca domestica* males seem to see their mates from some distance and fly directly to them, lighting on the back of the mate. Here sight would seem to play considerable part, and in *Fucellia* still more convincing evidence was obtained from observation of violent courtship of a fly which was separated by thick glass from the courter. Not only did this male court the other fly, but when she walked around rather rapidly, he very accurately followed her on the other side of the glass. This has been observed twice.

Since the wings play such a conspicuous part in courtship I was led to try the effect of cutting them off. Two males of the same age were used, the wings of one being cut off at the base. These were kept in the same vial for several days, and then placed with a virgin female several days old. The vial was then watched until copulation took place. This has been done 125 times, using different individuals each time. The normal male paired 72 times, the clipped male 53 times. As in all the similar experiments here reported care was taken to have the competing flies as nearly the same age and size as possible. The result indicates that there is very slight, if any, selection against the clipped males. It seemed possible that courtship made the female ready to copulate, but that she would then mate with either male. To test this hypothesis another series of experiments was carried out. A single pair of flies was placed in each vial, using each day an equal number of normal and of clipped males. The length of time before copulation was recorded in each case. A preliminary account of this experiment has been published by Morgan ('13); but the data used there have been discarded, since two serious sources of error had not then been recognized. It was not realized that the time before copulation might be influenced by a previous copulation having occurred in the same vial; and sufficient precautions against drying were not taken—a very important factor. A new series of experiments, in which these points were controlled, gave the results shown in table II. As a matter of fact, however, these data are very similar to the discarded series.

TABLE II

Minutes before Copulation	Number of times observed	
	Normal ♂	Clipped ♂
0– 3	15	4
4– 6	19	9
7– 9	10	7
10–12	15	5
13–15	3	7
16–18	8	4
19–21	3	10
22–24	3	4
25–27	9	4
28–30	2	2
31–33	2	2
34–36	0	4
37–39	1	2
40–42	3	2
43–45	2	1
46 and over, including failures	43	73

This table seems to justify the suspicion that led to the experiment. Had the females discriminated against the clipped males to the extent shown above when both kinds were present, the normal males would certainly have appeared at a greater advantage. That the result was not due to less activity on the part of the clipped males is indicated both by the contests described above and by the following observations. In some of the experiments recorded in table II the number of minutes before courtship began was observed. Table III indicates that the clipped males began courting as quickly as did the normals.

TABLE III

Minutes before Courtship	Normal	Clipped
1– 2	12	9
3– 4	2	3
5– 6	1	2
7– 8	1	2
9–10	0	1
11–12	1	0
13 and over	7	7

From these experiments it seems certain that the wings are of value in courtship; but the effect probably is to produce sexual excitement in the female, rather than to cause her to select a male that uses his wings. No " choice " is involved; but, as pointed out by Watson ('14, p. 173), the effect, in nature, would be strongly in favor of the normal male.

It seems probable that touch is of considerable importance in the sexual process, and all my observations are consistent with that view, but I have no direct experimental evidence to that effect. It is not possible to get evidence from *Drosophila* such as Kellogg obtained from *Bombyx*, because the flies are more active, and less easily sexually excited, than is the silk-worm moth.

Two kinds of experiments have been carried out in an effort to find out what part of the body is responsible for causing sexual excitement. A female without an abdomen, but alive and active, was placed with males that had been isolated from other females for four days. She was vigorously courted.

Three gynandromorphs have been tested to determine their sexual behavior. None showed any certain indications of male behavior, but all were vigorously courted by males. Of these three gynandromorphs the external characters were as follows: (A) All female, except one side of the head, which was male; (B) female on one side of the whole body, male on the other side; (C) female, except the genitalia, which were male. It is doubtful what conclusion, if any, is to be drawn from these few observations.

SEXUAL SELECTION—ARTIFICIAL ABNORMALITIES

The male of *Drosophila ampelophila* bears a small comb on his front metatarsi, a secondary sexual character not found in most species of the genus.[7] Lutz ('11) has shown that the removal of this comb has no effect upon the availability of males for copulation. That is, the females were not influenced by the sex-comb in their choice of mates.

It sometimes seems to be difficult for the male to get the wings of the female out of his way so that he can mount her. For this reason I carried out an experiment the converse of one recorded above; using two virgin females of the same age, one with normal wings, the other with wings removed. These were put with a normal male. In 52 successful trials the normal female was paired with 25 times, the clipped one 27. Again it would seem as though clipping the wings has very little if any effect.

SEXUAL SELECTION—MUTANTS

Lutz ('11) found that certain slight abnormalities in wing venation were selected against both by normal and abnormal flies of both sexes. The abnormal flies were not noticeably different from the normals in behavior, so that it seems quite unlikely that the results were due to a difference in the activity of the two types. Moreover, if, let us say, the normal male was more active than the abnormal, so that he would be more likely to pair first, it would seem that the normal female would not be so easily paired with as the abnormal; or *vice versa*, if we suppose the abnormal female to be less active and therefore more likely to be paired with, it is hard to see why the abnormal male should be at a disadvantage. Further evidence bearing out this view of the effect of differences in activity will be given below. Lutz suggested that it seems unlikely that sight could have any influence, and that perhaps there is some unpleasant smell correlated with the abnormality, this being the basis of selection.

I have conducted a series of experiments upon some of Morgan's *Drosophila* mutants, in an effort to find if there was any selective mating in connection with them. The following mutants were used:

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[7] So far as my observation goes it is present only in *D. ampelophila*, *D. confusa*, *D. obscura*, and three or four undescribed species.

(1) White eyes. This form was first described by Morgan ('10). There is no color in the eye. This probably means that the fly is blind, and it has often been observed to be less strongly phototactic than the wild fly. White eyed flies are also less active and vigorous than normals.

(2) Yellow body color. Described by Morgan ('11). The whole body of this fly is lighter than that of the normals, and there is a distinct yellow color to the wings. Sight seems to be normal, but again the flies are not so active as are the normals.

(3) Curved wings. The main interest of this form in this connection is that the wings are always held extended, in somewhat the same position as that of the courting males. The flies are perhaps a little less active than the normals

(4) Vermilion eyes. Described first by Morgan ('11a). These flies differ from the normals in that the eyes are of a brighter and less intense red. Their vigor and activity is very little, if at all, inferior to that of the normals.

Some of the flies used had yellow bodies and white eyes, and in one experiment a few vermilion eyed yellow black colored females were used. This latter combination was at the time considered one of the weakest stocks in the laboratory, and was used for that reason.

The method of the experiment was as described above for the wing clipping experiment. For instance, a white eyed female would be given her choice between a red male and a white one of the same age and size. Then the experimenter simply watched until pairing was seen, and the flies were then thrown away. The following table (IV) gives the results obtained.

TABLE IV

Red vs. white eyes. (Normal body color.)

"Chooser"	"Chosen"	Number of cases
Red ♂	Red ♀	54
	White ♀	82
White ♂	Red ♀	40
	White ♀	93
Red ♀	Red ♂	53
	White ♂	14
White ♀	Red ♂	62
	White ♂	19

TABLE IV—*Continued*

Gray (normal) vs. yellow body color. (Red eyes.)		
Gray ♂	Gray ♀	25
	Yellow ♀	31
Yellow ♂	Gray ♀	12
	Yellow ♀	30
Gray ♀	Gray ♂	60
	Yellow ♂	12
Yellow ♀	Gray ♂	25
	Yellow ♂	8
Vermilion Black-yellow ♀	Red-gray ♂	13
	White-gray ♂	1
Gray and yellow body colors. (White eyes.)		
Gray ♂	Gray ♀	11
	Yellow ♀	4
Gray ♀	Gray ♂	21
	Yellow ♂	3
Red and white eyes. (Yellow body color.)		
Red ♂	Red ♀	3
	White ♀	4
White ♂	Red ♀	9
	White ♀	9
Red ♀	Red ♂	9
	White ♂	2
White ♀	Red ♂	21
	White ♂	1
Red and vermilion eyes. (Gray body color.)		
Red ♂	Red ♀	7
	Vermilion ♀	5
Vermilion ♂	Red ♀	4
	Vermilion ♀	4
Red ♀	Red ♂	11
	Vermilion ♂	14
Long and curved wings. (Other characters normal.)		
Long ♂	Long ♀	10
	Curved ♀	13
Curved ♂	Long ♀	5
	Curved ♀	3
Long ♀	Long ♂	14
	Curved ♂	4
Curved ♀	Long ♂	9
	Curved ♂	5

It appears that sexual selection is not involved in any of these cases. The impression gained from observation of over 1,000 " contests " of this sort is that the outcome is not a matter of choice. A female, in the great majority of cases, seems to allow the first active amorous male that comes along to pair with her; or, if she is disinclined to mate, resists all males apparently indifferently. When a male is sexually excited he pairs with the first female he finds which will allow him to. As a result, the more active and vigorous males are likely to win their contests, and the greater the difference in vigor, the greater the proportion of times the better male wins. This is just what the results show to happen. So far as the small numbers show, the vermilion male is at no disadvantage and the curved male is not quite able to hold his own, while it is certain that the yellow and white are far behind their normal opponents.

In the converse case, a less vigorous female will be less likely to resist or escape from the male successfully if she be disinclined to mate. But this influence should have less effect on the result than the one discussed above, since both females will often be willing to mate and will not try to escape. This again agrees exactly with the facts as given above.

The two results of unequal vigor discussed above seem to me quite adequate to explain all the results obtained. There is no evidence of any " choice " on the part either of males or of females. Unlike the abnormal venation studied by Lutz, these mutants probably have no significance from the point of view of sexual selection, in the narrower sense of that term.

SUMMARY

Experiments indicate that sight is not essential in sex recognition in *Drosophlia*. The olfactory and tactile senses are probably both concerned, as in most other insects.

The wings of the male play a conspicuous part in normal courtship. Experiments with males from which the wings had been removed indicated that the function of these organs in courtship is the production of sexual excitement in the female.

Experiments were carried out with four mutants (white eyes, vermilion eyes, yellow body color, and curved wings), involving the observation of 839 contested matings.

As a result of these experiments it seems probable that the

four characters involved have no selective value, except in so far as results from the fact that at least two of these classes are less active then normals.

In general it is probable that, in *Drosophila*, neither sex exercises any " choice " in the selection of a mate. A female that is ready to mate will accept any male, and a male that is ready to mate will do so with the first female that will allow him to.

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THE WHITE RAT AND THE MAZE PROBLEM

IV. THE NUMBER AND DISTRIBUTION OF ERRORS—A COMPARATIVE STUDY

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What is the maze problem? It is the learning of a difficult path, having many blind alleys, under a stimulus so strong and certain that finally, when put into the labyrinth, the animal runs swiftly and surely to the goal without error. It consists of a series of movements which tend toward a definite end and which are so ordered that the position and the direction of the turns seem to be the all important factors. The animal's task is to learn this motor co-ordination, ours, if possible, to find out how it does it.

In the learning of the maze we find not a single problem but a complex of many and much light has been thrown upon them through the work of Small, Watson, Richardson, Carr and others. Some of the questions which arise in the course of such investigations are, however, still without satisfactory answers. The preceding numbers of this series have dealt with the problems of sensory control in the maze. This paper attempts to deal, briefly, with some of the more general features of the maze problem in the light of that experimentation. One question which immediately suggested itself concerned the relative value of the different senses when directive in such a problem.

THE RELATIVE EFFECTIVENESS OF THE DIFFERENT SENSES AS MODES OF CONTROL

This comparison is not an easy one to make since any one sense factor is never isolated but only emphasized in the sensory complex. The following table (I) shows factual data taken in different ways from the learning scores. If we turn this into terms of per cent, making the lowest and therefore best score always 100, and basing the others on this we get table II. By normal maze is meant the unpainted wooden maze where the

TABLE I

	Time of learning	Average errors first 5 trials	Average errors last 5 trials	Total average errors per animal	Average time first 5 trials	Average time last 5 trials	Surplus time
Normal maze...	12.1 ±3.6 trial	48.7 ±7.7	.1 ±.14	66.6±16.	16.3±6.7 min.	.31±.05 min.	93.9±16.5 min.
Olfactory maze, trail in true path.........	8.1 ±2.4 trial	13.2 ±2.9	.04±.04	20.5±5.6	8.7±3.9 min.	.28±.08 min.	64.9±23.6 min.
Composite black-white maze.........	14. ±11. trial	17.4 ±4.5	.3 ±.4	34.6 ±8.4	7.6±4. min.	.4 ±.1 min.	47. ±16.8 min.
Cutaneous maze (sides on)	16.5 ±3.7 trial	30. ±12.8	.18±.21	51. ±23.	1.8±2.7 min.	.18±.06 min.	15.3 ±6. min.
Cutaneous maze (open).......	16.5 ±6.6 trial	21. ±5.2	.09±.11	37.3 ±5.1	1.9 ±.7 min.	.15±.03 min.	13.9 ±4.3 min.

TABLE II

COMPARISON OF NORMAL, BLACK-WHITE AND OLFACTORY MAZES

Time of learning
Olfactory 100%, Normal 145%, Black-white 175%

Accuracy
Initial—Olfactory 100%, Black-white 130%, Normal 370%
Final— Olfactory 100%, Normal 250%, Black-white 750%
Total— Olfactory 100%, Black-white 175%, Normal 330%

Time
Initial— Black-white 100%, Olfactory 115%, Normal 215%
Final— Olfactory 100%, Normal 110%, Black-white 143%
Surplus—Black-white 100%, Olfactory 138%, Normal 190%

COMPARISON OF OPEN MAZE WITH ENCLOSED NORMAL MAZE OF SAME PATTERN

Time of learning
Open maze 100%, Normal 100%

Accuracy
Initial—Open maze 100%, Normal 150%
Final— Open maze 100%, Normal 225%
Total— Open maze 100%, Normal 140%

Time
Initial—Normal 100%, Open maze 105%
Final— Open maze 100%, Normal 120%
Total— Open maze 100%, Normal 110%

sides to the alleys were high enough to prevent any outlook to the neighboring runways and the light and odor were as evenly distributed as possible. The second maze was of the same plan but the true and the false paths were made to differ decidedly in brightness values. The third maze, again of the same pattern, had an olfactory trail in the true path.[1] The figures from the open maze are not compared directly with the others but with the score from the same maze when the restraining walls to the alleys were in place.[2]

We will not stop to comment upon the time of learning, as the chief differences are seen in the accuracy records. The olfactory maze heads the list in this respect both in initial, final and total accuracy within the limits of the experiment. The black-white maze follows second in initial accuracy and in total, because of the initial, but falls far behind in final accuracy.

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[1] In these tables the combined black-white figures are used, i.e., two groups of animals of five each where the true path was white and the *cul de sacs* black, and two groups of the same size where the conditions were reversed. The olfactory records are those where the trail was in the true path since this seemed most typical for our purpose. The combined olfactory scores make but little difference in the rating, they simply somewhat lowered the scores in the early trials and raised them in the final. For full details consult the previous papers.

[2] These mazes are all described in previous papers.

The reasons for this have been discussed in another paper. The time records are almost a direct reflection of the accuracy for, although the final scores distinctly favor the olfactory and black-white mazes, the advantage is but slight. The cutaneous open maze is also better than the normal in all of the accuracy counts, and also in final and total time. The small differences in time again are probably more or less an expression of the accuracy with a balance in favor of the open maze.

In these results, then, the olfactory maze leads, the open maze stands next in order while the black-white and the normal mazes approach each other very closely if all of the counts are considered. It will be seen that the big advantages which these sensory mazes offer are found in the early trials, in the setting up of the automatisms, and that the apparent total gain is due, for the most part, to the gain in the early trials. The established habit is practically the same no matter under what sensory conditions it is set up. The distracting effects of some of these sensory situations which affect the final scores are discussed in the previous papers.

Why some experimental workers should choose to neglect the error records is still a mystery to some of us. Certainly the real differences in the bits of learning given above are not shown by the time records. It is more essential in the normal life of a rat that it should be able to thread a beam or a cornice without falling, to jump from one projection to another without missing, to avoid being cornered and to strike its hole exactly when pursued by its enemies than to run a certain number of feet per second. The total distance which has been a measurement warmly advocated has advantages but it does not show really significant variations from the true path, although there is always, we will grant, a relation between the total number and amount of the errors and this total distance. If a rat always took the shortest way home, if it did not have its own peculiar way of getting out from its hole, perhaps this measure would express the facts more truly. The animal runs out into the maze a little way, runs back, runs out a little farther and then back, etc. This is a purely instinctive activity quite on a par with those natural movements in and about a rat's hole that insure it an open way home and such actions may not at all signify that the path as far as traversed is not familiar.

These runs then, which are included in the total distance, are not of the same nature as those other errors which take it entirely off the trail. They indicate its method of learning. They are interesting of course, and perhaps valuable for learning but they are not of the same class as the others. In all of this work, since our interest lay in the ability which the animals possessed to follow or to neglect a certain sensory stimulus, the errors consisted in leaving the true path. But it is not alone the number and kind of errors which excite our interest in this problem but also the distribution of the errors within the maze itself.

DISTRIBUTION OF ERRORS

The following tables show the distribution of errors in the different mazes. Whether a *cul de sac* will be entered or not depends upon the general direction in which it extends, its relation to the food box and whether it is so placed that the animal enters it headlong, etc., etc. For these reasons and for the sake of fairness we have chosen to compare the total scores of alleys 1, 2 and 3 with the corresponding error scores of 5, 6 and 7,[3] in the Hampton Court Maze. The normal maze record shows a greater score on every count for the first three than for the last three alleys. The combined black-white maze table reveals the same thing, as does also the cutaneous normal records. In the cutaneous maze, alleys 4 and 5 were very near to the food box, so near that in the open maze the animals sometimes succeeded in jumping across. For this reason these alleys were very attractive and the different results in the open maze may, perhaps, be explained in this way. It will be observed, however, that in the last three counts in the open maze also, when the automatism is beginning to be perfected, favor the final alleys. The olfactory maze, where the trail is in the true path, gives a record where the conditions are reversed, but when the trail is in the alleys the normal standard is again approached although the degree of difference between the first three and the last three alleys is less. The elimination of the final members of the series first is not only true of the groups as a whole but also of the individual animals. The records of 41 rats in the normal, black-white and cutaneous groups were gone over and only five rats found where the relation was reversed and two where they were the same. The number might have been easily doubled but it seemed useless to do so.

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[3] The *cul de sacs* are numbered in the order in which they occur in the maze.

TABLE III
Distribution of Errors, Normal Maze

	Alley 1	Alley 2	Alley 3	Alley 4	Alley 5	Alley 6	Alley 7	Alleys 1, 2, 3	Alleys 5, 6, 7
Total errors............	81	112	146	82	68	121	25	309	214
Trial at which the error was not made three times in succession by any rat..............	18	21	26	5	13	16	11	31.6	13—
Average errors per rat after 10th trial........	1.1	1.5	2.2	.7	1.2	1.	.6	1.6	.9
Average error per rat from 20th to 35th trial.	.3	.9	1.	.3	.2	.1	.1	.7	.1

TABLE IV
Distribution of Errors, Black-white Maze

	Alley 1	Alley 2	Alley 3	Alley 4	Alley 5	Alley 6	Alley 7	Alleys 1, 2, 3	Alleys 5, 6, 7
Total errors............	31	55	45	43	11	24	5	131	40
Trial at which the error was not made three times in succession by any rat..............	16	19	7.5	9	4.5	6	2.5	14.2	4.3
Average errors per rat after the 10th trial....	.6	1.7	.8	.6	.1	.1	.1	1.	.11
Average errors per rat from 20th to 35th trial.	.2	.6	.3	.5	.1	.05	.15	.36	.1

TABLE V
Distribution of Errors, Olfactory Maze, Trail in True Path

	Alley 1	Alley 2	Alley 3	Alley 4	Alley 5	Alley 6	Alley 7	Alleys 1, 2, 3	Alleys 5, 6, 7
Total errors............	1	14	12	16	14	36	17	27	57
Trial at which the error was not made by any rat three times in succession...............	1	11	17	16	10	14	9	9+	11
Average errors per rat after the 10th trial....	0	0	1.1	.9	0	.3	.3	.4—	.3—
Average errors per rat from 20th to 35th trial.	0	0	.5	.1	0	0	.1	.16	.03

TABLE VI
DISTRIBUTION OF ERRORS, OLFACTORY MAZE, TRAIL IN THE *Cul de sacs*

	Alley 1	Alley 2	Alley 3	Alley 4	Alley 5	Alley 6	Alley 7	Alleys 1, 2, 3	Alleys 5, 6, 7
Total errors............	0	40	59	62	35	73	22	99	130
Trial at which the error was not made by any rat three times in succession...............	0	7	32	6	5	10	8	13	7+
Average errors per rat after the 10th trial....	0	2.1	2.3	5.3	2.3	1.6	.3	1.46	1.4
Average error per rat from the 20th to the 35th trial............	0	1	1.5	4.6	1.1	1.	.1	.83	.7

TABLE VII
DISTRIBUTION OF ERRORS, CUTANEOUS MAZE—SIDES ENCLOSED

	Alley 1	Alley 2	Alley 3	Alley 4	Alley 5	Alley 6	Alleys 1, 2, 3	Alleys 4, 5, 6
Total errors.................	53	25	52	60	19	1	130	80
Trial at which the error was not made three times in succession by any rat......	26	17	18	23	8	2	20.3	11.
Average errors per rat after the 10th trial.............	2.6	.8	1.6	2.1	.5	.1	1.6	.9
Average errors per rat from the 20th to the 35th trial......	.8	0	.6	.6	0	0	.5	.2

TABLE VIII
DISTRIBUTION OF ERRORS, CUTANEOUS, OPEN MAZE

	Alley 1	Alley 2	Alley 3	Alley 4	Alley 5	Alley 6	Alleys 1, 2, 3	Alleys 4, 5, 6
Total errors.................	30	29	48	66	37	4	107	107
Trial at which the error was not made by any rat three times in succession.........	33	17	17	25	10	2	22.3	12.3
Average errors per rat after the 10th trial............	3	2.5	2.3	3.1	2.6	.3	2.6	2.
Average errors per rat from the 20th to the 35th trial......	1.6	1.3	1.3	.6	1.1	0	1.4	.5+

In a normal maze, when the *cul de sacs* are at all comparable, the number and persistence of the errors of the first part of the series may be explained by the laws of association, i.e., they are made first, made most frequently and therefore persist longer. On the other hand, it may be that the food box as the final and probably the strongest member of the motor series may become more directive and react back into and help to organize the later members of the series most closely connected with it in time much as other memory series—not motor—are known to be organized.

The black-white maze influenced the distribution of errors but as the rat's vision is notoriously poor the influence was chiefly seen in the smaller amount of difference between the records of the first and the last *cul de sacs* as the character of the distribution remained the same.

In the open maze the errors were more evenly distributed for the reasons given above. The animals in the olfactory maze were really learning to follow a trail and incidentally learning a motor series. The incidental errors increased toward the end of the series although the last two counts show a balance in favor of 5, 6 and 7. The experiment when the trail was in the *cul de sacs* gave a situation where the true path resembled that of the normal maze but the *cul de sacs* were made more attractive because of the odor and thus influenced the totals. The last three counts, however, are lower for 5, 6 and 7 in this experiment also.

Sensory clues in these mazes, not only favor accuracy but also affect the distribution of the errors among the members of the series of blind alleys. The influence is seen both in the degree of difference and in the character of the distribution. The distribution could be said to be less mechanical and not quite so predictable as in the normal maze although on the whole the relations were similar in all of the mazes.[4] The final members of the *cul de sacs* were entered less frequently and eliminated first.

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[4] Since making these tabulations and comparisons Miss Hubbert's paper has appeared, "Elimination of errors in the maze," *Jour. Animal Behav.*, Vol. 5, No. 1. Her results contradict those reported here, but this work must stand on its own merits. I cannot at this place enter into a discussion of Miss H's. paper. It scarcely seems fair, however, when there are so few *cul de sacs*, to eliminate the first and the last, where the chief differences are seen, from the comparison. There is always overlapping in the middle of any series. If the nature of the maze compelled this elimination then no general conclusions should be drawn.

Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy at Harvard College, No. 262

THE GRASPING ORGAN OF DENDROCOELUM LACTEUM

ELIZABETH S. P. REDFIELD

The grasping organ of Dendrocoelum lacteum is situated on the ventral surface of the anterior part of the head of this worm, between its two auricular appendages.

Ijima ('84) records this organ as used for locomotion against currents. Gamble ('96, pp. 35-48) describes this species as "affixing a sucker, placed on the under side of the head, to the substratum, and pulling the posterior end close to this. The sucker, discovered by Leydig, is even better developed in (Planaria) punctata, P. mrazekii, and P. cavatiça, and is an efficient adhering-organ, which has probably been developed from a similar but simpler structure found in a considerable number of both fresh-water and marine Triclads."

How far these interpretations apply to Dendrocoelum lacteum, will appear in the following account. This paper is based on an experimental study of the function of the grasping organ in Dendrocoelum lacteum, and I wish to thank Dr. G. H. Parker, under whom the work has been done, for his kind assistance.

STRUCTURE OF THE GRASPING ORGAN

The grasping organ of Dendrocoelum lacteum, when studied under a low power of the microscope, appears as two symmetrically placed opaque thickenings, near the middle of the anterior margin of the head. In the resting condition, these structures project forward very slightly, forming a pair of rounded lobes, as shown in figure 1, *A*.

As the planarian moves about in ordinary locomotion, this organ is in continual activity, stretching out, contracting, now grasping an object, now rejecting it. When grasping at materials these lobes are stretched forward fully twice their resting length and press the object, one on each side (fig. 1, *B*). The form of

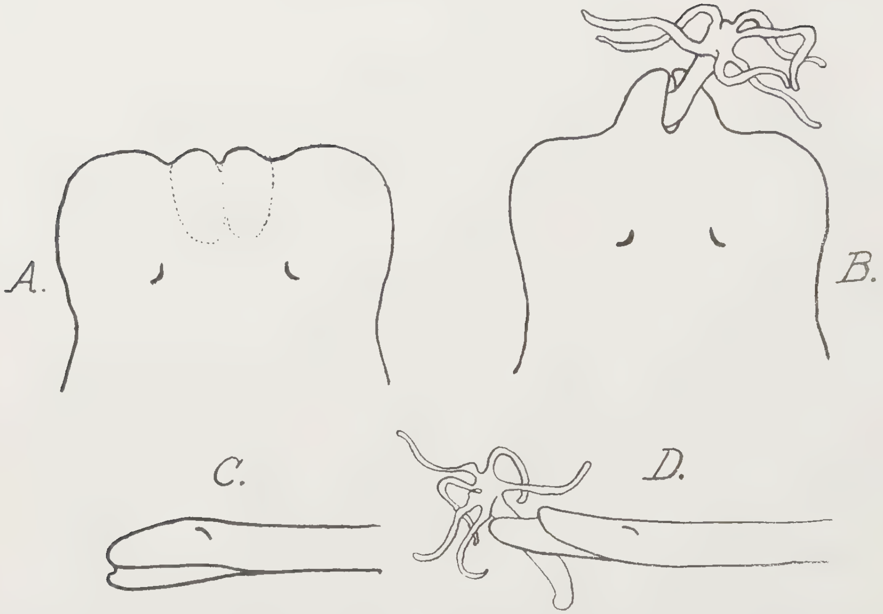

FIGURE 1. Head of Dendrocoelum; *A* and *B*, dorsal views; *A*, grasping organ contracted; *B*, grasping organ expanded; *C* and *D*, lateral views; *C*, grasping organ contracted; *D*, grasping organ expanded. Magnified 25 diam.

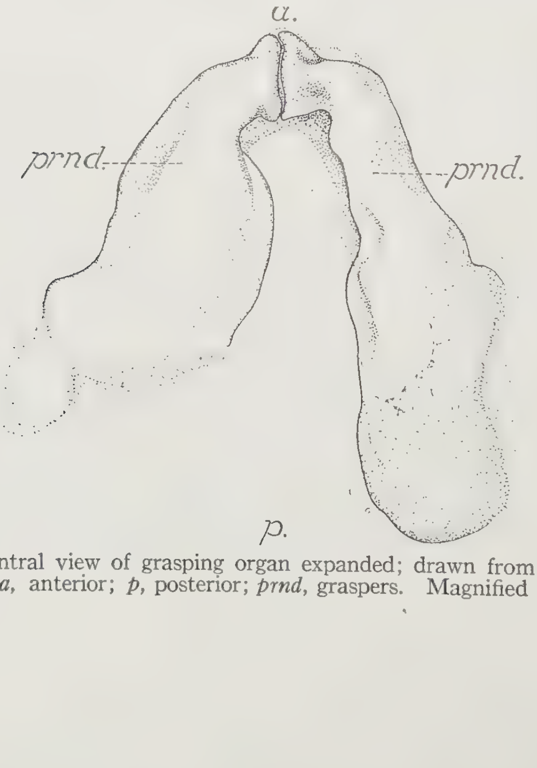

FIGURE 2. Ventral view of grasping organ expanded; drawn from a wax reconstruction; *a*, anterior; *p*, posterior; *prnd*, graspers. Magnified 50 diam.

the grasping organ as seen in surface view, is well represented in figure 2. It was with great difficulty that a planarian was killed with the grasping organ extended, and the preparation from which figure 2 was drawn was the only one in perhaps a hundred to show the organ favorably.

The organ consists of two ridges on the ventral side of the head, which converge abruptly and meet as two thickened, club-shaped lips at the anterior end. Posteriorly the ridges become broad and low, and merge into the ventral surfaces of the head.

Evidently this specimen was fixed in a condition of semi-extension, for a transverse section of another Dendrocoelum (fig. 3) shows the median groove to be greatly narrowed and the ridges on either side to be folded together.

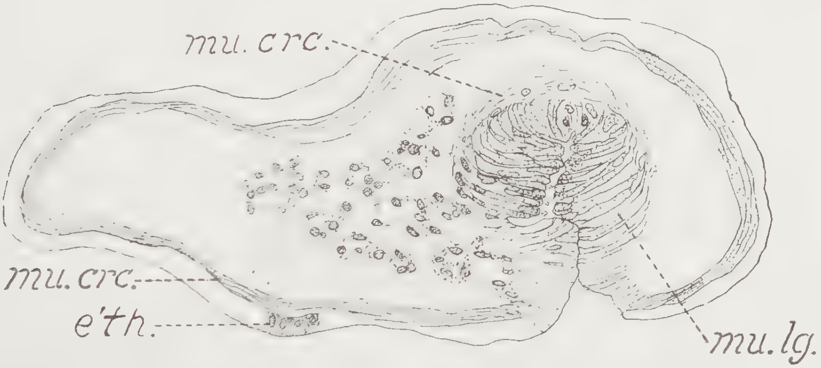

FIGURE 3. Transverse section of grasping organ showing musculature; *mu. crc.* circular muscles; *e'th.* epithelium; *mu. lg.* longitudinal muscles. Magnified 75 diam.

There are no rigid structures to be discovered in sections of the grasping organ. Such sections show an abundance of muscular tissue (fig. 3). It would appear probable that the grasping organ is extended through the action of these muscles upon the body fluids, thus producing a pressure which would stretch the anterior part of the ridges and perhaps give to the head an upward turn, thus bringing the ventral ridges into an anterior position. Figure 1, *C* and *D*, illustrate how this action may take place. The movement is too quick to allow of very accurate analysis, but it is evident from the way in which this organ is used and from the structure as seen in figure 1, that it is more appropriately designated a grasping organ, than a sucker.

FUNCTIONS OF THE GRASPING ORGAN

Certain classes of materials, such as substances suitable for food, call forth in Dendrocoelum a very striking reaction, which involves the grasping organ. If, for example, a pair of forceps which has been dipped in a twenty per cent cane-sugar solution is held in front of a Dendrocoelum, the animal will suddenly dart its head forward and seize the forceps with the grasping organ, and adhere to them so firmly that the creature can be shaken loose only with difficulty. The word " pounce " describes this reaction more vividly than any other, and the idea of a pouncing worm can surprise the reader no more than the reaction did the author.

A moving bait will call forth this reaction more readily than a motionless one. Living Hydra, and pieces of meat are seized by Dendrocoelum lacteum in this manner. These facts suggest that the grasping organ is used to capture and hold the prey of the planarian, until the pharynx can be affixed and feeding begin. To ascertain whether the grasping organ was primarily concerned with feeding, the following experiment was tried. A solution of brown sugar, which was visible in water, was applied by a capillary tube to various regions on the surface of the worm. On stimulating the lateral edges there was a local expansion of the body, a condition to be observed anywhere between the posterior end and any point almost as far anterior as the auricular appendages. In the neighborhood of these appendages, the application of the sugar solution caused the head to be turned towards the region of stimulation, the grasping organ to seize the end of the capillary tube, and feeding to begin.

Animals tested in this way with a capillary tube containing only water instead of brown-sugar solution, gave no reaction, and consequently the responses to the sugar solution could not be regarded as due to the mechanical disturbance produced by the slight current of water. From this experiment, it seems clear that the receptors which initiate the feeding reaction of the worm are located upon its head.

As a further test of this conclusion, the following experiments were made. Worms from which the brain, eyes, and auricular appendages had been removed by decapitation, were put each in a Syracuse watch-glass full of water and left standing twenty-four hours. A twenty per cent brown-sugar solution was then applied from a capillary tube to their lateral margins. In no case was there a response of the whole worm, as when feeding begins, though in each instance a local expansion of the side of the body occurred where the sugar solution had been applied. As a preliminary experiment, before removing their heads, all the worms were tested with a brown-sugar solution, and found to feed upon it in a normal manner. The heads of the decapitated worms were kept, each in a watch glass, and subjected to the same stimulus as that used on the trunk of the worm. They responded by coming up to the tube and remaining close to it, the grasping organ being agitated in the same manner as in the normal worm about to begin feeding. Occasionally a head would circle away from the tube but it always came back again.

These experiments confirm the previous one, in that they show that the receptors for the feeding reactions are located upon the head of the worm. One might object to drawing this conclusion on the grounds that animals whose heads had been removed might be expected, as a result of the operation, to fail to respond normally; but since the heads, which had been subjected to as great a shock as the trunks, if not a greater one, reacted normally, this objection can have no weight. In order to determine whether the grasping organ itself, or the auricular appendages were the receptors, the following experiment was tried.

The grasping organ, after having been stimulated to action, was removed by catching it with forceps and pulling it out. The results were surprisingly uniform; worms without the grasping organ did not attempt to feed. It would appear from this experiment that the receptors for the feeding reflex, are located probably on the sucker itself.

Mechanical and certain chemical stimuli (as a twenty per cent solution of sodium chloride) call forth a rapid forward movement of the animal, like that of some leeches, produced by (1) extending the body, (2) attaching the grasping organ to the substratum, (3) releasing the posterior end, contracting the body, (4) attaching the posterior end, and then again (5) carrying the body forward, thus repeating the whole operation. If the grasping organ is removed, the animal may still progress in a leech-like manner, attaching itself by the action of the general ventral surface of the anterior end combined with that of the margins of the body in the same region. If the head is cut off, the animal can also still progress in a leech-like manner. Consequently the grasping organ is not essential for this mode of locomotion. Animals in a dish of water held in a current, attach themselves to the substratum by the tail, but not by the grasping organ, thus showing that the grasping organ is not used to prevent the animal from being washed away.

In my own experiments, however, there is nothing to show that the grasping organ may not be used for locomotion; the point insisted upon is the importance of its relation to feeding.

SUMMARY

From the foregoing it is evident that the grasping organ of Dendrocoelum lacteum is primarily employed by the animal in feeding. This grasping organ is used to seize and hold material on which Dendrocoelum lacteum feeds. It is stimulated to activity by appropriate materials applied to the receptors located on the anterior part of the worm. The grasping organ may be used in certain forms of locomotion, but it is not essential to this operation.

POSTSCRIPT

Since the completion of this paper, a note by Julius Wilhelmi, Einige biologische Beobachtungen an Süsswassertricladen, has been published in the Zoologischer Anzeiger, Bd. 45, pp. 475-479, in which these grasping reactions are recorded.

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THE HABITS AND NATURAL HISTORY OF THE BACKSWIMMERS NOTONECTIDAE

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The purpose of this article is to record observations made on the aquatic Hemiptera Notonectidae. These insects were chosen for the experimental work because they are found in great abundance and because very little is known about their behavior. The work was done in the Zoological Laboratory of the University of California under Professor S. J. Holmes, to whom I wish to express my gratitude for kind suggestions and criticisms. Thanks are also due to Professor C. E. Van Dyke for his help in determining the species.

The Notonectidae are commonly known as backswimmers from their habit of swimming on their backs. They are widely distributed, extending from the arctic to the tropical regions. Kirkaldy has recorded about twenty different species of Notonectas. According to J. R. de la Torre, Bueno, twelve of these species are peculiar to America. The bugs here described were collected in a small pond on the university grounds, the species identified being four in number, *Notonecta insulata* Kirby, *Notonecta undulata*, variety *Charon*, *Notonecta indica*, and an unidentified species. The last named is most abundantly represented. *Notonecta insulata* is the largest of the four species, ranging in size from five to five-tenths mm. in width. It is usually of a dark or bluish-black color. *Notonecta undulata* and *Notonecta indica* are smaller and more slender than *Notonecta insulata.* Notonectas show many striking adaptations to aquatic life: their backs are convex and boat-shaped, the ventral surface being flat. The hind legs are long, specially flattened and fringed, thus serving as oars. The two pairs of forelegs are sparsely covered with hairs and are provided with claws. The latter serve for the capture of food and for attachment to the surface film, from which they hang with their heads downward, the posterior part of the ventral surface being exposed to the air. When in this position the fore- and middle-legs are slightly bent so that the claws are at the surface. The insects often rest at the bottom, clinging to sticks or weeds.

It is also interesting to note that the hairs of the body are so arranged as to facilitate respiration. On the forelegs are two rows of hairs pointing in opposite directions, and partly covering the spiracles on the thorax. The ventral surface of the thorax has a double row of thick hairs on both sides of the margin, pointing posteriorly and meeting the hairs of the abdomen. There is also a double row of hairs on each lateral margin of the abdomen; the hairs of the outer rows increase in length as they approach the posterior end of the abdomen, where they end in one row of long tufts. The inner rows of marginal hairs cover the pleura and can be flapped back by the contraction of the abdomen. The carina or the ventral midpart of the abdomen is thickly covered with hairs which extend laterally on both sides and overlap the hairs from the lateral margin, which extend toward the middle line. Thus the rows of hairs form a waterproof covering over the gutters which lie one on each side of the carina and serve for the conveyance of air. In addition to the rows of long hairs described, the whole surface of the abdomen is covered with short hairs. On the dorsal surface, beneath the wings, there is a row of hairs between each segment, pointing posteriorly, while fine hairs cover the entire dorsal surface of the abdomen. The hairs are covered with an oily secretion which prevents their getting wet.

Three pairs of spiracles are found on the thorax, and a pair on each segment of the abdomen in the pleura. The air finds entrance to the spiracles from the posterior end of the body, where an opening is formed by the tufts of hairs as soon as the animal reaches the surface of the water. The hairs cling together and close the opening as soon as the animal is submerged. Sometimes the whole fringe is lifted like a lid from the pleura when the animal reaches the surface of the water, closing again as soon as it sinks. The bug comes to the surface to receive a fresh supply of oxygen and to emit carbon dioxide. The bug being surrounded by air, is lighter than the water so that it is compelled to keep the rowing legs in constant motion in order to keep beneath the surface. As soon as the leg-motion ceases, the air buoys the insect up until it meets the surface film. As soon as the animal is suspended by the surface film, it begins to move its forelegs. Hoppe suggests that by moving the legs the insect forces the air into the spiracles in the thorax. I am rather inclined to believe that it is trying to straighten out the hairs and to brush away the impurities, because the animal performs these movements every time some foreign substance is dropped on the thorax. If a small particle of asphalt be placed on the thorax, the animal moves the legs in an effort to free itself from it, and if it can reach the part, will also use the beak for the same purpose. It brushes the ventral and dorsal surfaces of the abdomen with the hind legs, and especially the tip and lateral margins.

Notonecta, if sealed in water, dies within from three to five hours. In this case it hangs to the surface film all the time with its body covered with gas bubbles. If a drop of oil is put on the ventral surface of its body, the creature dies immediately. If the backswimmer is sealed in the water from which the oxygen has been expelled by boiling, death results in from five to ten minutes. If the water is left exposed to the air, the insect clings to the surface film almost constantly, with the fringes lifted and the breathing pores exposed, while under ordinary circumstances it comes to the surface only once in every thirty or forty minutes. On a dry substratum, if exposed to sunshine, the insect dies within forty or fifty minutes; in a cool and shady place it can live much longer.

In several books on insects the statement is made that Notonectidae bury their eggs in the stems of plants. I have found that this is not the case in any one of the species studied. The ova are usually deposited and glued on sticks or on the stems of plants. Very often I have found the eggs deposited on the backs of other insects, such as dragonfly larvae, and on the walls of the aquarium. Soft sticks were placed in the aquarium. The eggs, however, were never found buried in the stems, but were always deposited in rows around the sticks. In the process of ovoposition, the female attaches herself to the lower surface of the stick and moves the posterior segments very vigorously until the egg is extruded and attached, then she moves away. Frequently embryos are found in a row with their heads pointing in the same direction. If the eggs are examined immediately after they have been deposited, the surrounding gluing substance is very plainly seen. The eggs are beautifully white, elongated, and cylindrical, with the attached side slightly flattened. The chorion is decorated with small depressions. The eggs of *Notonecta insulata* are about two mm. long. Those of smaller species are slightly smaller in size. After an incubation period of twenty days, the chorion splits at the anterior end and the nymph crawls out. In working out from the envelope the nymph first gets its head out, contracting and expanding the body and bending over it pulls itself out of the case, sometimes stopping to rest, then continuing the process again. Inside the coarse egg envelope and surrounding the nymph is a thin transparent membrane which occasionally breaks, allowing the animal to escape while the membrane remains attached to the outer envelope, but often the nymph is still surrounded by the membrane after leaving the egg-case and must work its way out from it. As soon as the nymph is free it goes to the bottom and rests a while and then begins to move about actively, searching for food. The nymphs are very beautiful, with large compound eyes which are conspicuously red. The body is transparent white. The long hairs are well developed on the lateral margins and over the pleura, which are shallower than in the adult; the hairs on the middle carina are short and irregular. After from seven to ten days the first moult takes place. Hoppe states that there are five complete series of moultings in *Notonecta glauca*, and J. R. de la Torre, Bueno,thinks that there are about five moultings in all the species. I have not been able to follow the complete series of moultings, because it is extremely difficult to raise nymphs in an aquarium owing to the fact that they attack one another even in the presence of an abundance of food. They are very sensitive to foul air and contaminated water. The nymphs differ from adults in their behavior in that they come more frequently to the surface, about once in every three or five minutes, and the fringes are usually flapped back, while in the adult the fringes are lifted only when the insect is in great need of oxygen.

The food of Notonectas consist of animal matter, chiefly, living or dead insects, but they do not hesitate to attack other animals. Thus Bueno has observed the nymphs of *Notonecta* *undulata* kill and suck the juices of young fish which had just emerged from the eggs. I have seen the nymphs and adults kill young *Diemyctylus torosus* as soon as they emerged from the gelatinous envelope. I have also observed a nymph dragging a Diemyctylus larva which was about three times its own size. The nymphs usually attack May-fly larvae and drag them about, although the latter are twice the size of the aggressor. The larger species usually attack the smaller ones and the young are eaten by the adults, being seemingly preferred to other kinds of food. *Notonecta* nymphs of equal age and size attack each other and suck each others juices during their attack until one or both are dead. They often attack dragonfly nymphs, which are many times their own size, usually approaching from beneath, grasping them with the forelegs and piercing the body with the proboscis. The nymph has no chance of escape from the insect, the latter continuing its hold no matter what position the victim may assume. The dragonfly nymph does not die from the first attack but only after a number of punctures. *Notonecta* is also destructive to young fish.

The Notonectidae are not easily affected by chemicals, as they may live in strong sodium chloride solution without showing any change in activity. They can live in five per cent alcohol for days. They become drowsy in twenty per cent alcohol, but if put in pure water they revive again. Several specimens were kept in strong copper sulphate solution for several weeks and did not suffer from it, while other animals dropped in the same liquid died within a few minutes. A Notonecta insulata was kept alive in Gilson's fixing fluid over two hours.

Notonectas are positively phototactic and can be led by the light in any direction. If an aquarium containing Notonectas is left in the sunshine, the bugs move quickly to the lighted end of the tank, and fly toward the light, producing a buzzing sound. If the aquarium is placed between two lights of different intensities, the Notonectas usually collect near the light of greater intensity, as is shown in the following table:

Two lights, one of one hundred candle power, the other of thirty-two candle power, were placed one at each end of the aquarium. Every five minutes the lights were reversed and the insects moving toward each light counted.

One hundred candle power	Thirty-two candle power
29	5
30	4
29	5
27	7
34	0
30	4
29	5
24	10
31	3
30	0
25	9
21	13
25	9
23	11
23	11
26	8
28	6
31	3
20	14

If Notonectas are put in a high jar and light admitted from below, the bugs are more numerous at the bottom. If the light shines from above, the bugs are more numerous on the surface. This proves that Notonectas have a strong positive phototaxis. However, their phototaxis may be modified by some such factors as temperature. Thus, an increase in temperature results in an increase in phototaxis, as shown in table following:

Number of Notonectas, thirty-four. Two lights, one sixteen candle power, the other one hundred candle power, were placed at either end of the aquarium and were turned on alternately every five minutes and the animals counted. The number moving toward the light is indicated by a plus sign, those moving away or at random, by a minus sign. Temperature increased gradually.

Weak light		Temperature	Strong light	
+	—		+	—
18	16	16°	30	4
15	23		24	10
28	6	18°	30	4
30	0		29	5
32	2	20°	33	1
32	2		34	0
33	1	22°	34	0
32	2		34	0
34	0	24°	34	0
34	0		34	0
34	0	26°	34	0

34	0		34	0
34	0	28°	34	0
34	0		34	0
34	0	30°	34	0
34	0		34	0
34	0	32°	34	0
34	0		34	0

At temperature of sixteen to eighteen degrees the insects are slower in their motions. At a temperature of twenty to twenty-two degrees they become more active, and with a further increase of temperature they are still more active, moving toward the light hurriedly and remaining crowded there. In a temperature of thirty-two degrees and above, the water bugs are slower in their movements, dying in a temperature of forty to forty-two degrees.

With increasing need for oxygen as is the case when Notonectas are placed in a high jar which is kept in diffused light and the temperature gradually increased, the bugs always come to the surface. But if the jar, containing the insects, is put in a dark room and a light is placed below the jar and then the temperature gradually increased as before, the bugs, attracted by the light, remain at the bottom, becoming more and more positively phototactic with the increase of the temperature, beating their heads against the bottom of the aquarium until they die in an effort to get nearer the light. Rarely one or more escape from the center of attraction and rise to the surface. If, however, two lights are placed, one above, the other below the aquarium, and the temperature gradually increased, the backswimmers rise to the surface and remain there even after the light above has been turned off, regardless of the fact that the light below is still shining. The last experiment indicates that although the creatures are strongly positively phototactic, after they have departed once from the source of light, the need of oxygen overcomes their phototaxis.

The question arises, Why do the insects rise to the surface with the increase of temperature ? As I have explained above, the animals carry air under the hair surrounding the body and in the spacious air tubes. Thus they are rendered lighter than the water and must keep their appendages in motion in order to keep beneath the surface. The increase in temperature brings with it an increase in the activity of the animal with a resultant greater need for oxygen for the metabolic changes which are taking place, hence the bugs rise to the surface in order to obtain the oxygen from the atmosphere. That the bugs remain at the bottom of the aquarium in spite of the high temperature, indicates that there are two opposite forces in action, viz., the need of oxygen and the positive phototaxis. The latter is increased with the increase of the temperature and is evidently so strong that the animals, after they have once been attracted by the light, can not depart, but struggle to get to the light at the bottom until they die, while, after they have once departed from the source of light the tendency of the bugs, with the increase in temperature, is to gather at the upper light. And even after the upper light is extinguished and the lower light is shining, the bugs still persist in remaining at the surface, because the demand for oxygen is greater than the positive phototaxis. The bugs are probably led by instinct to seek the surface when they become aware of the need of oxygen, and again they are only led by their strong positive phototaxis to go to the bottom of the aquarium. In normal conditions the Notonectas rise to the surface at more or less regular intervals. The same is true in diffused light when the temperature is increased, the bugs always rise to the surface and remain there. The buoyant force plays an important rôle here, but it may be of secondary importance only.

If the insects are sealed in ordinary water, they first swim about, but later they remain at the surface all the time. They may go down for a moment but return immediately to the surface, usually remaining there until they die.

If Notonectas are sealed in water from which the oxygen has been expelled by boiling, the air carried by the bugs is absorbed by the water, hence the insects drop to the bottom and do not rise, although they try hard to reach the surface. In this condition they die in from five to ten minutes. In this case buoyant force is of least importance and it is only this specific response which leads the animals to the surface in their quest for oxygen.

If Notonectas are placed in boiled water in an open dish they immediately come to the surface, remaining there until the amount of oxygen in the water has increased. When a light was placed below the aquarium containing boiled water, the Notonectas collected around it, the majority of them dying in a few minutes, while a few repeatedly returned to the surface for oxygen, sometimes picking up their dead companions on the way and carrying them to the surface. These experiments were tried with adult Notonectas and with nymphs with the same results.

Cold does not destroy the phototaxis of Notonectas, but when the insects become chilled, they move more slowly toward the light. If kept in ice-water for some time, the insects become so chilled that they drop to the bottom. If the water is shallow the insects come to the surface when the temperature is increased but if the water is from fifteen to thirty cm. in depth, while they show signs of life as soon as the temperature of the water is increased, they fail in their attempts to reach the surface. Sometimes they succeed in rising a few inches, swimming obliquely, falling back after each successive effort. It is an interesting fact that, while under ordinary circumstances the bugs must be in a constant motion in order to remain beneath the surface, here the reverse is true, the bugs working in the greatest effort to reach the surface and falling back each time. Evidently they have lost their air in some way or another. Thus the animals may lie until an increase in temperature arouses them to greater activity. Metabolism goes on, the remaining oxygen is used up, and when the animals attempt to rise there is no surrounding air to buoy them up, and death from lack of oxygen is the result. While in shallower water they have more access to free oxygen and can more easily reach the surface of the water. Hoppe believes that the cold water dissolves the carbon dioxide more readily and that, therefore, the animals, losing the surrounding gas, are rendered heavier and sink down. The fact of the bugs' trying to reach the surface, leads one to believe that the effort is an instinctive one when the animals are in need of oxygen.

If Notonectas are exposed to an arc light they first show a tendency to negative phototaxis for a moment, then they fly to the light and are burned. Young nymphs are positively phototactic from the very first day. I have experimented with light reactions on Notonecta insulata which were only three or four hours old. When exposed to light in a dark room, they crowded to the lighted side of the aquarium.

Notonectas are negatively geotropic and are usually found at the surface when at rest. This, however, may be due to the fact that in an aquarium without any weeds or sticks the surface film serves as the only medium of attachment. A stronger evidence in favor of negative geotropism is that the bugs, when placed on the wall, always crawl upward. Again, when the bugs are placed in a high jar which is kept in diffused light or in perfect darkness, they always rise to the top as soon as the jar is reversed. But here we have to deal with two factors, the need of oxygen in the closed jar, and the negative geotaxis.

Notonectas are positively rheotactic, always swimming against the current. They have positive thigmotaxis and usually are attached to some object when at rest. Sometimes they are attached to one another, three or four in number.

SUMMARY

Notonectas are widely distributed. They are very voracious and attack animals many times their own size. The insects are well protected by the thick layer of surrounding air, hence chemicals have very little influence on them. Notonectas have a strong positive phototaxis. The phototaxis increases with the increase of the temperature and with greater light intensity. When exposed to arc light or to bright sunlight, they immediately take to their wings, flying toward the light. At a temperature of zero centigrade they become chilled, lose their air, and drop to the bottom of the aquarium and die if the aquarium is deep. They are positively rheotactic, always swimming against the current. The young hatch within twenty days and are well adapted to their environment from their very first day of life. They resemble the adults in their behavior and instincts.

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SOME OBSERVATIONS ON THE INTELLIGENCE OF THE CHIMPANZEE

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The observations reported in this paper were made on two chimpanzees; Peter, an ape on the vaudeville stage a few years ago, and Consul, also lately, and I believe still, on the stage. However, the writer is not certain that the latter ape exhibited on the stage as Consul and observed by the writer was the Consul extensively mentioned in the newspapers when brought from Europe a few years ago. The manager represented the latter vaudeville star to be the original Consul.

The observations made on Peter included those made at two performances by him on the stage and in one private examination of him. The observations on Consul included seeing him perform on the stage once and a private examination of him by the writer. In the cases of both Peter and Consul the observer questioned the keepers concerning the animal's performances, habits and training.

Of course, had it been practicable, observations should have been made much more extensively to give satisfactory results. But we believe that the observations reported warrant at least a partial explanation of the apparently superior intelligence exhibited by these and similar animals.

We shall first give a syllabus of the conclusions to which the observations appear to lead, and the indications to which the observed reactions seem to lead.

The writer believes that the apparently superior intelligence of the apes is principally accounted for by:

1. The superior motor-equipment of the animals
2. The training which all show animals receive.
3. The semi-erect carriage of apes.

We note also that:

4. There are indications of intelligent imitation in the mental make-up of the animals.

5. There are indications of a low form of reasoning, or of crude ideas in the apes.

6. There are indications of more human-like emotions than monkeys such as the Rhesus manifest, e.g., sympathy.

7. They show superior capacity for intelligent reactions to that of any of the lower orders of animals. Probably, largely on account of superior motor-equipment and their upright carriage.

8. With all allowances made, apes are superior in intelligence to all sub-humans and so are nearer to man than any of the other lower animals.

OBSERVATION OF PETER ON THE STAGE

Peter, dressed like a man, sat down to a table, put on a napkin and ate food with a knife and fork. After eating, he struck a match, lighted a candle, lighted a cigarette and smoked. He gave his keeper, McArdle, a light for the latter's cigarette from his own.

Upon command from the keeper, the ape danced on the stage fairly well, much like a man, a sort of jig-dance.

When roller-skates were put on his feet, he skated around the stage skilfully. He appeared to skate as well as a girl whom he chased around the stage.

The animal got upon a bicycle himself and rode it around the stage. He chased the girl around the stage while riding the wheel. While riding, he drank water from a cup handed him. Then he skilfully rode between a number of bottles and cut a sort of figure 8 while riding between the bottles. The ape picked up a bottle and drank out of it while riding.

The animal rode the bicycle up an inclined plane on the stage. I noticed that he always increased his speed just before coming to the inclined plane.

After performing these feats, Peter undressed and went to bed, very much like a man does.

PRIVATE EXAMINATION OF THE APE

Upon command from the keeper, Peter took up a hammer and a nail and drove the nail into the wall, quickly and without observable awkwardness.

IMITATION

As a test of imitation, I took out my watch and pressed on the stem, slowly, and opened the watch three times while Peter watched my actions with attention and apparently with interest. Then I reached it to him: he held it and pressed on the stem correctly several times, as if to open it. However, he did not press hard enough, and the watch did not open. He thereupon attempted to open it with his finger nails. The keeper stated to me that the ape had not received any training on that act.

APE WRITING

I held out a writing tablet and a pencil to Peter. He at once seized them and began scribbling, i.e., making irregular marks on the tablet. I made, in his sight, the letter T; a very plain T, with simply one vertical and one horizontal stroke of the pencil. The ape made a rather poor T, the first time shown. He also made a W when I showed him once. Peter seemed to like to use the pencil and tablet.

Upon being ordered by his keeper, the animal put a handkerchief around my neck and tied it quickly and correctly when told to do so. He also untied the knot quickly.

He came and slapped me on the lower limb when the keeper bade him, though apparently with some reluctance. The animal would lie down and sit up when ordered to do so.

APE LANGUAGE

When told to do so, Peter articulated the word "mama." The ape spoke the word something like a foreigner speaks it. I noted, however, that the wife of the keeper pressed her fingers against the ape's under lip when he spoke the word mentioned.

Now, let us attempt to analyze the factors in the apparently superior intelligence shown in the actions of the ape, just recited. In these acts, it seems we may see in the superior motor-equipment of the animal one of the principal factors. Peter's comparatively perfect hands enabled him to use the knife and fork in eating and to handle a cup in drinking. His man-like lower limbs, his hands and his upright figure enabled him to ride the bicycle, to pick up a bottle and drink while riding, etc. His superior motor-equipment was also, as it seems to the writer, a principal factor in such feats as driving a nail, tying a handkerchief in a knot and untying it, etc., Dogs and other animals, if they had the intelligence, lack the requisite motor-apparatus to do such acts.

Another principal factor in all these acts was, doubtless, training. We know that horses, dogs, and even pigs may be trained to do many feats.

In the writing by the ape, his man-like hands together with training, probably accounts for it, though imitation is possibly a factor here. What accounts for his seeming eagerness to mark on the paper might, however, be an interesting question. It might be interesting also to test how far the ape might be taught to carry his writing.

Peter's articulation of the word " mama " was very possibly quite mechanical and parrot-like, perhaps not understood by himself. However, it would be interesting to test how far such speaking by apes might be carried.

Peter's correct attempt to open the watch looks like intelligent imitation. However, though the keeper assured me that the ape had had no training in that act, we might doubt the statement. Then, perhaps, we could account for the reaction by the ape's hands, his training and the well known curiosity of all monkeys. If the veracity of the keeper can be relied upon, we have here, as it appears to the writer, a case of intelligent imitation.

In the matter of the ape increasing speed to ride up the inclined plane, if training does not account for it, we appear to see evidence of something very like ideation or reasoning of a low order. If in this instance ideas are present, they are perhaps what Hobhouse has named " practical ideas," i.e., crude and unanalyzed ideas. The writer is inclined to believe that the latter together with motor-equipment and training are the factors involved.

OBSERVATION OF CONSUL ON THE STAGE

Consul did most of the feats which Peter had done, such as putting on a napkin and eating at a table, getting upon a bicycle and riding around the stage, riding between nine bottles, riding up an inclined plane. Consul did these acts in a similar manner.

The latter ape also performed some other feats: He poured out his coffee, picked his teeth, cleaned his teeth with a brush, cleaned his tooth-brush. He rode a wheel with a lamp on his head, held by himself while riding; he bored with an augur, put the rounds in and fitted together a ladder, with some help. He took a tablet and pencil and wrote, or the keeper said he wrote; I do not know what he wrote. He took down the receiver of a telephone and listened, or appeared to listen. The ape used a typewriter, that is, he pressed on the keys, so far as the writer could judge, and can remember, perhaps without knowing what he wrote.

Consul threaded a needle, cut paper into strips with scissors. He took a key and locked and unlocked a padlock, and did other acts requiring similar intelligence.

These acts by Consul, like similar acts by Peter, are perhaps accounted for principally by the animals' motor-equipment, erect carriage, and training. Some of them, such as riding up the inclined plane and increasing his speed to go up, again raise the question of ideation or a lower form of reasoning in the animals' mental make-up.

IN PRIVATE EXAMINATION

The writer did not note in Consul the good nature and sympathy shown by Peter. The former ape showed the brute in him by a certain roughness of manner and by not obeying his keeper very readily, etc.

In this connection we might mention that Peter showed evidences of affection for his keeper by such acts as putting his arm around the latter in a very human-like manner and kissing him. When I questioned Peter's keeper as to sympathy, etc., in apes, to let me see for myself, the keeper, in the ape's sight, pretended to have hurt his hand, whereupon Peter went to him, put his arm around McArdle, and by his acts gave very evident signs of ape sympathy. Peter acted in a similar manner when I also pretended to have hurt my hand.

From the actions which have been enumerated of these two chimpanzees, we may, as the writer believes, venture to conclude that:

1. The apparently superior intelligence of the chimpanzee is accounted for principally by;

(a) Superior motor-equipment.

(b) Training.

(c) Their semi-erect and biped position.[1]

2. There are some indications of ideas of a crude and unanalyzed character or of a lower form of reasoning in their mental equipment.

3. That whatever are the factors involved in their reactions, apes such as the chimpanzee are the most intelligent sub-humans of which we have knowledge. As anatomically they are superior to the lower orders of animals, by the criterion of structure as indication of intelligence, they should be more intelligent than their humbler congeners.

We must, as already stated, admit that more extensive observations should have been made on the individuals we have considered. More individuals should also be observed and experimented upon before drawing final conclusions on some of the points at least involved.

However, the present writer cannot but believe that these and similar apes are the most intelligent of the sub-humans. We feel that anyone who has observed their actions, who bears in mind their anatomical superiority—their physical structure as compared to that of any lower forms on the one hand and to that of man on the other—who has noted their semi-human looks and actions in general, cannot but agree with this latter conclusion.

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[1] NOTE.—As a corollary from (a) and (c) doubtless, the superior intelligence of other lower species of monkeys is accounted for in part by their motor-equipment.

THE HABITS OF THE WATER-STRIDER GERRIS REMIGES

CHRISTINE ESSENBERG

From the Zoological Laboratory of the University of California

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INTRODUCTION

The purpose of this article is to report the results of observations made of the aquatic Hemipteran *Gerris remiges*. This work was carried on in the Zoological Laboratory of the University of California under the direction of Professor Samuel J. Holmes, to whom I am indebted for many valuable suggestions and criticisms. I also wish to express my gratitude to Professor C. E. Van Dyke for help given in determining the species.

The Gerridae, commonly known as water-striders, are of world-wide distribution and include many different species. The specimens were collected from small pools in Strawberry Canyon, near the University Campus, Berkeley. They are dark brown in color, the dorsal surface of the abdomen being red. The ventral surface is usually gray and is furnished with a plush-like coating which repels the water. The nymphs are much shorter with bodies closely resembling those of adults, but with the plush-like coating not so well developed. The water-striders pass the winter as adults, hibernating under logs, rocks, rubbish, and in other sheltered places. In the early spring they emerge, lay eggs along the edge of grasses growing under water but near the surface, fastening them with a waterproof glue. The eggs hatch within three weeks.

These insects move backward and forward with equal facility, though the usual direction of locomotion is forward; but if the animal is approached from the front it moves backward very swiftly. It can also float on its back as has been observed taking place in the aquarium during and after the cleaning process of the insect, when it lies on its back for a considerable time and is carried by the water, moving its legs or else keeping perfectly quiet. When disturbed while on the water the insects betake themselves quickly to the land or among the weeds, and hide by clinging to the lower surface of the leaves or by lying quietly on the ground.

For its food supply the water-strider depends upon such living or dead insects as it finds floating on the surface of the water. Sometimes it catches mosquitoes flying above the water. In the latter case it sits quietly upon some aquatic plant and, as soon as the mosquito approaches, makes a swift leap and catches the insect, or when a mosquito is discovered at some distance on the surface of the water, the water-strider moves very swiftly towards it until it reaches its victim, when it seizes it with its raptorial forefeet. The food is never taken from under the water. Several individuals were kept in an aquarium thickly populated with mosquito larvae, although the insects had not received any food for several days and were in a starving condition, they did not touch the mosquito larvae, but as soon as a mosquito emerged from the pupa case it was caught and eaten. *Gerris remiges* is very voracious and will eat any animal matter, not disdaining its own kind. It does not hesitate to attack animals many times its own size. In the aquarium, where there is less chance of escape, the young nymphs usually fall victims to the adults, and the stronger ones, as a rule, feed upon their weaker companions. In the laboratory the water-striders were fed mostly upon flies, they being most easily obtained, but they ate other animal matter, such as ants, bees, butterflies, moths, Jerusalem crickets, etc. *Gerris remiges* is not particular in its choice of food and its sense of taste is not well developed. Upon different occasions the insects were fed flies, some of which had been previously soaked in quinine and alcohol and some, in coal oil. They first approached the flies carefully, then left them, but soon returned and attacked them in spite of the taste or odor. Three days later these same insects were fed flies which had been soaked in ammonia for twenty-four hours. The following morning they were dead. The insect attacks fresh and decaying matter indiscriminately.

Gerris remiges can live on land as well as in water. It runs with a jerking motion, making from four to six jumps in succession and then making a short stop. Very often it turns a sommersault and continues running without interrupting its course until it reaches a place of safety. There it lies quietly for from fifteen to twenty-five minutes, then suddenly begins its race again. The insect can right itself when placed on its back by turning over longitudinally, resting its body on the head or abdomen. If a water-strider is held up by some of its legs, it tries to free itself by pushing the object holding it with the remaining free legs, at the same time pulling the legs which are being held.

The water-strider is accustomed to cleaning itself and some times is engaged in this occupation for hours. It rubs one leg with another, then it rubs its proboscis and the ventral and dorsal surface of the body interchangeably. Very often it rolls over in the water during the cleaning process. If some foreign substance, such as dust or asphalt is put on the dorsal surface of the body the animal dives and rubs itself in the greatest effort to get rid of the substance. If the insect is left in a weak light it remains quiet excepting that it rubs its legs; if brought into a strong light, it swims towards the source of light as nearly as possible, and rubs its legs.

Feigning death is a characteristic of this insect, which is especially well developed in some individuals. In accomplishing this feat it crosses its forelegs and becomes perfectly rigid. It may be rolled on the floor, picked up and held by one leg, dashed with water, exposed to considerable heat or to strong light without showing any signs of life. If left alone it lies quietly for ten or fifteen minutes, then gradually livens up and begins to run. If touched, it again feigns death, and thus it may continue for hours. The insect can be artificially made to assume this condition by putting it on its back and holding the hind legs, at the same time gently tapping it on its ventral surface, or by holding it down and pressing on the dorsal surface. The first sign of death feigning is usually the crossing of the forelegs, then the body becomes rigid and the legs are drawn up close to it so that the whole body assumes a compact shape. The water-strider has been made to assume this position thirteen times in succession. Later it did not so readily respond to the stimulus and the successive periods of death feigning gradually decreased in length, the first periods lasting for from twenty-six to twenty-five minutes and the last periods lasting for from six to five minutes, only. The larvae of these insects are especially prone to feign death. When taken from the water they sometimes feign death and do not recover for an hour or longer. Feigning death is evidently not a voluntary act on the part of the animal, this condition being brought about by some physiological change. Professor S. J. Holmes cites similar experiences with *Ranatra fusca* also with some birds from which he pulled feathers while the birds were in this condition without producing any response.

Gerris remiges is positively phototactic. If it takes to its wings once in a while it always flies toward the light, producing a buzzing sound as it flies. When placed in an aquarium it swims toward light. It is more phototactic in strong light and in high temperature, less so in a weaker light.

Gerris remiges is negatively geotropic. If an individual is left in an empty jar it always crawls upward. If placed on the wall it crawls upward, never downward, although it may jump or fly to the ground. The same is true when it retires to sleep on plants, attaching itself to the lower surface of the plants, with head pointing upward. Although very swift of motion when on water, the insect remains perfectly motionless on plants and makes no effort to escape when picked up. Blind individuals act in the same way as do the normal ones in regard to geotropism, i.e., they crawl upward or opposite to the source of gravity.

Water-striders are positively thigmotactic, piling up in three or four layers, sometimes becoming so tangled up in their long legs that it becomes difficult for those in the middle to disentangle from the others. They also crowd together when frightened and when hibernating in the winter.

The water-striders are positively rheotactic and always swim against the current. Experiments have been tried with individuals in which one or both eyes were destroyed. When water was rotated in a dish they swam against the current.

The sense of smell of the water-strider was tested in the following way: A small drop of coal oil was placed on the upper edge of the wall of the aquarium upon which the insects were trying to climb. When they had almost reached the oil, which was gradually moving downward, they stopped, moved their antennae, bent backward and plunged into the water. This experiment was tried with coal oil and ammonia water interchangeably, the insects commonly responding in the same way. A drop of coal oil was placed on the surface of the water in a corner of the aquarium. When the insects, in calmly gliding around occasionally came near the oil, they stopped, moved their antennae, then retreated. When frightened and in rapid motion they sometimes came directly into the field of the oil, when they would swim back excitedly and try to escape by jumping at the walls of the aquarium at the opposite end.

These insects seem to have a sense of hearing. When, for instance, a door is slammed, or some loud metallic sound is produced, the animals immediately respond by moving backward. When wingless flies are dropped into the water and are buzzing, the water-striders hurriedly move toward them, while a dead fly may float for a considerable length of time without being discovered. This experiment was tried with *Gerris remiges* whose eyes had been destroyed, with the same result, the blind insects moving from all directions toward the source of sound. However, they do not respond to all sound equally well. A tuning pipe was attached to one end of a wire, the other end of which was in the aquarium. The tuning pipe was then blown, but it had little or no effect on the water-striders, which continued their movements at random on the surface of the water.

SUMMARY

Gerris remiges are very common and are widely distributed. They are found almost everywhere on the surface of the water, beneath the rocks and in crevices. They are swift of motion, moving forward and backward with equal facility. They are very voracious and carniverous, although they never attack animals below the surface of the water, but only those on the surface or on plants. They show no particular choice in the selection of food, eating any dead or living animal matter. If nothing is obtainable, they can live without food for weeks or months. They are specially given to the cleaning habit and may be engaged in this process for hours in succession. They are prone to feign death and may be artificially stimulated to do so several times in succession. They are positively phototactic.

Gerris remiges is positively thigmotactic, hence, usually found in groups or piles beneath rubbish and rocks. The insects also crowd together on the surface of the water. They are positively rheotactic and negatively geotactic.

.They seem to have some sense of smell. Their sense of hearing is not well developed, but they detect a sudden jar, such as the slamming of a door, or drumming on the edge of the aquarium, etc.

The sense of sight is keenly developed, the insects detecting a moving object or a shadow very quickly.

In considering the economic aspect, these insects may be useful because of their contribution to the reduction of the number of mosquitoes which lay their eggs on the surface of the water, also because of their destroying the emerging young mosquito.

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NOTES

MATERNAL INSTINCT IN A MONKEY

ROBERT M. YERKES

To my friend and fellow investigator, Doctor G. V. Hamilton, I owe the opportunity to make the observations of the behavior of monkeys which it is the purpose of this note to report. Gladly I avail myself of this chance to thank him publicly for his generosity in placing his animals and experimental equipment wholly at my disposal during the present year, and for his unfailing kindness and sympathy.

On February 27 one of the monkeys of our collection gave birth, in the cages at Montecito, to a male infant. The mother is a *Macacus cynomolgus rhesus* who has been described by Hamilton[1] as "Monkey 9, Gertie, *M. cynomolgus rhesus*. Age 3 years, 2 months. (She is now, May 1, 1915, 4 years and 6 months). Daughter of monkeys 3 and 10. First pregnancy began September, 1913." The result of this pregnancy was, I am informed, a still-birth.

The second pregnancy, which shall now especially concern us, resulted likewise in a still-birth. Parturition occurred Saturday night, and the writer first observed the behavior of the mother the following Monday morning. In the meantime the laboratory attendant had obtained the data upon which I base the above statements.

At the time of parturition Gertie was in a 6 by 6 by 12 foot out-door cage containing a small shelter box, with an exceptionally quiet and gentle male (not the father of the infant) who is designated in Hamilton's paper as Monkey 28, Scotty.

My notes record the following, exceptionally interesting and genetically important behavior. On March 1, when I approached her cage, Gertie was sitting on the floor with the infant held in one hand while she fingered its eyelids and eyes with the other.

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[1] Hamilton, G. V. A study of sexual tendencies in monkeys and baboons. *Jour. of Animal Behavior,* 1914, **5**, 298.

Scotty sat close beside her watching intently. When disturbed by me the mother carried her infant to a shelf at the top of the cage. Repeatedly attempts were made to remove the dead baby, but they were futile because Gertie either held it in her hands or sat close beside it ready to seize it at the slightest disturbance.

Especially noteworthy on this, the second day after the birth of the infant, are the male's, as well as the female's, keen interest in the body and their frequent examinations of the eyes, as if in attempts to open them. Often, also, the mother searched the body for fleas.

Observations were made from day to day, and each day opportunity was sought to remove the body without seriously frightening or exciting the female. No such opportunity came, and during the second week the corpse so far decomposed that, with constant handling and licking by the adults, it rapidly wore away. By the third week there remained only the shriveled skin covering a few fragments of bone, and the open skull from the cavity of which the brain had been removed. This the mother never lost sight of: even when eating she either held it in one hand or foot, or laid it beside her within easy reach.

Gradually this remnant became still further reduced until on March 31 there existed only a strip of dry skin about four inches long with a tail-like appendage of nearly the same length.

The male, Scotty, on this date was removed to another cage. Gertie made a great fuss, jumping about excitedly and uttering plaintive cries when she discovered that her mate was gone. Whenever I approached her cage she scurried into the shelter box and stayed there while I was near. This behavior I never before had observed. It continued for two days. On April 2, it was noted that she had lost her recently acquired shyness and she no longer made any attempts to avoid me. As usual, on this date, she was carrying the remnant about with her.

The following day, April 3, Gertie was lured from her cage to a large adjoining compartment for certain experimental observations. After she had been returned to her own cage the remnant was noticed on the floor of the large cage. I picked it up. Gertie evidently noticed my act, for although at a distance of at least ten feet from me, she made a sharp outcry and sprang to the side of the cage nearest me. I held the piece of skin (it looked more like a bit of rat skin than the remains of a monkey) out to her and she immediately seized it and rushed with it to the shelf at the top of the cage.

Two days later the remnant was missing, and careful search failed to discover it in the cage. It is probable that Gertie had carelessly left it lying on the floor whence it was washed out when the cages were cleaned. On this date Gertie seemed quieter than for weeks previously.

Thus it appears that during a period of five weeks the instinct to protect her offspring impelled this monkey to carry its gradually vanishing remains about with her and to watch over them so assiduously that it was utterly impossible to take them from her except by force.

After reading this note in manuscript, Doctor Hamilton informed me that Gertie had behaved toward her first still-birth as toward her second. And, further, that Grace, a baboon, also carried a still-birth about for weeks.

I am now heartily glad that my early efforts to remove the corpse were futile, for this record of the persistence of maternal behavior seems to me of very unusual interest to the genetic psychologist.

A REPLY TO PROFESSOR COLE

WALTER S. HUNTER

I cannot permit Professor L. W. Cole's recent article in the Mar.—Apr. number of this Journal, entitled "The Chicago experiments with raccoons" to stand unprotested. Abstracting from the deplorable tone of the publication, I should like to draw attention to one or two points only. (1) Professor Cole interprets my position as a desertion of the sensory-motor hypothesis in favor of some vague imageless thought construct. I tried strenuously in the monograph on Delayed Reactions to make clear that the ideational function ascribed to raccoons and to the child F was of a strictly sensory content. This content in any case need not be visual. It is not necessary that mental content copy the stimulus in order to represent it. In the Delayed Reaction experiments the content could not be visual because a visual *sensation* cannot be revived or reproduced. The content of the representative factor was very probably kinaesthetic (Delayed Reaction, p. 75) and was associated with the light. These kinaesthetic sensations could be revived and used as cues to differential responses. This is mentioned in many places in the monograph and is summarized finally in the classes of animal learning on page 79. I can see no grounds for so odd a misinterpretation of my attitude. (2) Professor Cole is aghast at the use of the term "steeple" for "staple" on page 18 of my monograph. This error was probably due to a slip in the proof reading. Had Professor Cole read a few lines further down the same page, he would have found the perfectly proper usage. (3) On page 167 of his article, by quoting a portion only of a sentence which in its turn was in a vital context, Professor Cole grossly misrepresents my statements concerning odor controls. It is to be noted that a very different criticism is involved to that offered elsewhere by Professor Watson. (4) The only confirmation that my work offers of Professor Cole's is, I still believe, the agreement indicated on page 20 of my monograph.

I see no need for further comments either upon the Delayed Reaction or upon the work by Gregg and McPheeters.